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Trophic interactions and consequent impacts of the invasive fish *Pseudorasbora parva* in a native aquatic foodweb: a field investigation in the UK

J. Robert Britton · Gareth D. Davies · Chris Harrod

Abstract Introduction of the invasive Asian cyprinid fish *Pseudorasbora parva* into a 0.3 ha pond in England with a fish assemblage that included *Cyprinus carpio*, *Rutilus rutilus* and *Scardinius erythrophthalmus* resulted in their establishment of a numerically dominant population in only 2 years; density estimates exceeded 60 ind. m^{-2} and they comprised >99% of fish present. Stable isotope analysis (SIA) revealed significant trophic overlap between *P. parva*, *R. rutilus* and *C. carpio*, a shift associated with significantly depressed somatic growth in *R. rutilus*. Despite these changes, fish community composition remained similar between the ponds. Comparison with SIA values collected from an adjacent pond free of *P. parva* revealed a simplified food web in *P. parva* presence, but with an apparent trophic position shift for several fishes, including *S. erythrophthalmus* which appeared to assimilate energy at a higher trophic level, probably through *P. parva* consumption. The marked isotopic shifts shown in all taxa in the *P. parva* invaded pond (^{13}C-enriched, ^{15}N depleted) were indicative of a shift to a cyanobacteria-dominated phytoplankton community. These findings provide an increased understanding of the ecological consequences of the ongoing *P. parva* invasion of European freshwater ecosystems.

Keywords Topmouth gudgeon · *Cyprinus carpio* · *Rutilus rutilus* · *Scardinius erythrophthalmus* · Trophic overlap · Stable isotope analysis · Angling

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Introduction

Biological invasions have been identified as agents of significant human-induced environmental changes and a threat to native fauna and flora (Vitousek et al. 1996). Ecological impacts range from single

prey-predator interactions between introduced and resident species (Clarkson et al. 2005; Dietrich et al. 2006; Bampfylde and Lewis 2007; Yonekura et al. 2007) to shifts in ecosystem function (Vander Zanden et al. 1999; Dietrich et al. 2006; Zimmerman and Vondracek 2007). Their detrimental impacts have generated interest in the factors controlling invasion success (Crawley 1987; Drake et al. 1989), the traits of successful invaders (Baker 1965; Rejmánek and Richardson 1996) and the types of communities most susceptible to invasion (Levine and D'Antonio 1999; Davis et al. 2000). In European freshwaters, these aspects are all highly relevant for topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel), as it is highly invasive and has recently been described as the continent's most invasive fish (Gozlan et al. 2005). This small (<100 mm) species of the Cyprinidae family, native to Japan, China, Korea and the River Amur basin (Pinder et al. 2005), is now widespread and locally abundant within favourable European habitats, and is considered a significant nuisance (Perdices and Doadrio 1992; Wildekamp et al. 1997; Pollux and Korosi 2006).

Following *P. parva* introduction, populations tend to establish rapidly and become numerically dominant in the fish community, provoking concerns of detrimental ecological impacts on native species through, for example, the potential for high competition for resources (Britton et al. 2007). It is also a healthy host of a pathogen identified as suppressing the growth and reproduction of other fishes, leading to mortalities (Gozlan et al. 2005). These concerns are, however, largely assumed and suffer from lack of empirical evidence and testing, despite production of a risk assessment that has identified them as high risk in UK waters (Baker et al. 2008) and their underpinning of a series of eradication exercises from UK lakes that has cost approximately £200,000 of public funds (Britton et al. 2008). Thus, the aim of this paper is provide increased knowledge on the ecological consequences of their introduction so that existing risk assessment protocols and management processes may be refined. Through use of a site that proved a natural mimic of the experimental conditions of a natural treatment (pond with *P. parva* introduction and rapid establishment) and control (pond with no *P. parva*), the ecological effects of the introduction of *P. parva* into an established aquatic food web for resident fishes were assessed. We examined the null hypothesis that the establishment of a sustainable population of *P. parva* and integration into the foodweb would not result in a measurable ecological impact on the resident fishes at the individual, population or community levels of biological organisation.

Materials and methods

The study was carried out on two adjacent ponds, one with *P. parva* introduction and one without, providing an 'experimental' pond (3,250 m^2 in area, maximum depth 3 m) and 'control' pond (3,060 m^2 in area, maximum depth 3 m) (Fig. 1). These were located in Worcestershire, England (N52°13'09''; W2°20'41''). They were dug in the late 1980s and once filled, a series of fish stockings were completed between 1990 and 1998 to provide fish communities comprising common carp *Cyprinus carpio* L., common bream *Abramis brama* (L.), roach *Rutilus rutilus* (L.), rudd *Scardinius erythrophthalmus* (L.) and gudgeon *Gobio gobio* (L.). No obligate piscivorous fish were introduced. Both ponds were oval in shape and had secchi-disk depths of between 10 and 15 cm, with minor differences observed between summer and winter. The species and density of riparian vegetation was similar between both ponds. Although both were used for recreational catch and release angling, pressure was minimal and primarily restricted to low numbers of anglers (<5) visiting the site each weekend between May and September. This fishery also operated strict limits on anglers introducing free offerings into the water, minimising the effects of angling practises on foodweb structure.

Pseudorasbora parva was accidentally introduced into the experimental pond in March 2003, with initial sampling in July 2005, using a 25 m seine net (2 mm mesh), confirming their establishment. Samples were then collected from both ponds between August 2005 and January 2006 using seine nets of up to 100 m length and 10 mm mesh for the purposes of this study. The ponds were then completely drained in February 2006 for a *P. parva* eradication exercise and all fish removed. These fish were then sorted, counted and weighed, providing an accurate estimate of density and biomass. From fish samples collected in August 2005, sub-samples from each pond were taken to the laboratory where fork length (mm) and mass (g) was recorded, scales collected and a sample

Fig. 1 Location of the study site in England and overview of the study site, where *1* = control pond and *2* = experimental pond

To River Teme

0.25 km
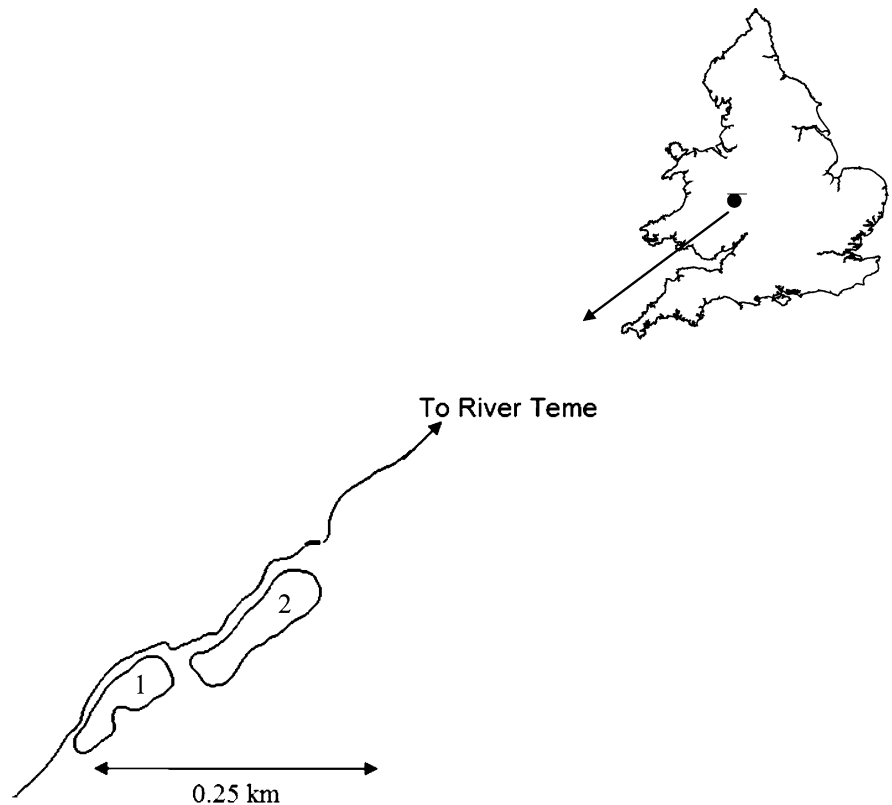
of dorsal muscle taken. These were to be used for both analysis of life history traits and foodweb structure.

To investigate foodweb structure, stable isotope analysis was completed on the fish muscle samples, with the baseline provided by invertebrate samples collected from each pond in September 2005. These were sampled using a combination of net tows in surface waters using a 250um mesh, sweeping pond nets through open water and by sieving (1 mm mesh) in situ from sediments gathered by an Ekman grab. Macro-invertebrate samples were of at least 20 individuals per family to reduce the effect of inter-individual variability. All samples for SIA were oven-dried at 60°C for 24 h, homogenised using an agate pestle and mortar, and stored in a desiccator prior to weighing into tin cups for SIA (typical mass = 0.55 mg). Carbon and nitrogen stable isotope ratios were determined via a Eurovector elemental analyser (Eurovector, Milan, Italy) coupled to a Micromass Isoprime continuous flow mass spectrometer (Micromass, Manchester, UK). Stable isotope ratios are given using the δ notation expressed in units per mil as

follows: δ (‰) = [(R sample/R standard) − 1] × 1000, and R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The reference materials used were secondary standards of known relation to the international standards of Vienna Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen. Repeated analysis of an internal fish standard (*R. rutilus*) indicated that precision for a single analysis was ±0.1‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$. Fish $\delta^{13}C$ data were arithmetically lipid-normalised according to Kiljunen et al. (2006).

Statistical comparisons of carbon and nitrogen stable isotope ratios were conducted using various approaches. To examine differences between ponds and species, mean (±95%) $\delta^{13}C$ and $\delta^{15}N$ values were calculated and plotted separately for each species in the control and experimental ponds. To provide a comparison of intraspecific differences between the two ponds, *t*-tests (unequal variances) were used to compare mean $\delta^{13}C$ and $\delta^{15}N$ values. To examine variation in the isotopic space inhabited by each species within and between ponds (Layman et al. 2007), MANOVA was used with $\delta^{13}C$ and $\delta^{15}N$ as dependent variables and pond and species as

independent variables, with examination of possible interactions between these. Where MANOVA indicated significant differences, GLM ANOVA (including Bonferroni-adjusted post-hoc tests) was used to compare mean canonical scores (calculated for the first canonical function of the MANOVA) to examine differences between species either within or between ponds. *P. parva* were excluded from the between-ponds analysis as they led to an unbalanced design, but were included in a separate MANOVA examining variation in $\delta^{13}C$ and $\delta^{15}N$ in the experimental pond. Finally, separate MANOVAs were run comparing the isotopic space inhabited by each species in the respective ponds.

To test the ecological consequences of *P. parva* introduction and establishment on the resident fishes, we investigated whether somatic growth rates changed in their presence. Ages from scales were determined by viewing under a projecting microscope ($\times 10$ to $\times 30$), with back-calculated lengths at age calculated using the body-proportion equation (Francis 1990). To compare growth between species, we compared residuals of length-age regressions to examine changes in fish size following *P. parva* invasion in the experimental pond by using fish sizes in the control pond as the control. This method was used due to statistical complications resulting from reliance on back-calculated lengths, i.e. repeated measurements from individual fish. To estimate mean fork length and identify changes following *P. parva* invasion, species-specific linear regressions of back-calculated fork length on age were completed and residuals stored. Note only fish of ages 1–5 years were used to utilise only the immediate pre- and post-invasion periods. Species-specific mean residual values, as mean fork length adjusted for age, were then compared between the two ponds and for the period pre- and post-invasion using 2-way ANOVA.

Results

The fish sample collected in July 2005 from the experimental pond revealed that an abundant population of *P. parva* had established following their introduction in March 2003. The draining of the pond in February 2006 revealed they were numerically dominant in the fish community, comprising >99% of all fish present (Table 1). The majority of *P. parva*

Table 1 Fish abundance of the control and experimental pond, February 2006

Species	Control pond	Experimental pond
Pseudorasbora parva		
Density (m^{-2})	0	59.7
Biomass (g m^{-2})	0	40.7
Length range (mm)	–	19–118
Cyprinus carpio		
Density (m^{-2})	0.1	0.1
Biomass (g m^{-2})	40.2	46.2
Length range (mm)	46–710	48–705
Rutilus rutilus		
Density (m^{-2})	0.4	0.3
Biomass (g m^{-2})	28.4	23.4
Length range (mm)	45–291	41–282
Scardinius erythrophthalmus		
Density (m^{-2})	0.2	0.2
Biomass (g m^{-2})	3.1	3.7
Length range (mm)	51–235	55–221
Abramis brama		
Density (m^{-2})	0.1	< 0.1
Biomass (g m^{-2})	2.1	1.6
Length range (mm)	85–355	81–365
Gobio gobio		
Density (m^{-2})	<0.1	0.1
Biomass (g m^{-2})	0.8	1.1
Length range (mm)	55–142	57–148

were between 20 and 40 mm fork length, with density in these size classes of approximately 40 m^{-2}. Other than the typically large-bodied *C. carpio*, *P. parva* had the highest biomass in the experimental pond. With the exception of *P. parva*, the composition and abundance of the fish community of the control pond was broadly similar, suggesting minimal impact of *P. parva* establishment at the community level at that time (Table 1).

In the fish community of the control pond, mean $\delta^{13}C$ values varied between -30.4 ‰ (*A. brama*) and -25.9‰ (*S. erythrophthalmus*; Fig. 2a; Table 2). Mean $\delta^{15}N$ values ranged between 11.4‰ (*S. erythrophthalmus*) and 13.6‰ (*G. gobio*). Examination of the isotopic biplot (Fig. 2a) indicated that this relatively simple fish community consisted of two trophic groups, one with relatively depleted $\delta^{13}C$ and enriched $\delta^{15}N$ values, and one with relatively enriched $\delta^{13}C$ and depleted $\delta^{15}N$ values. Comparison with
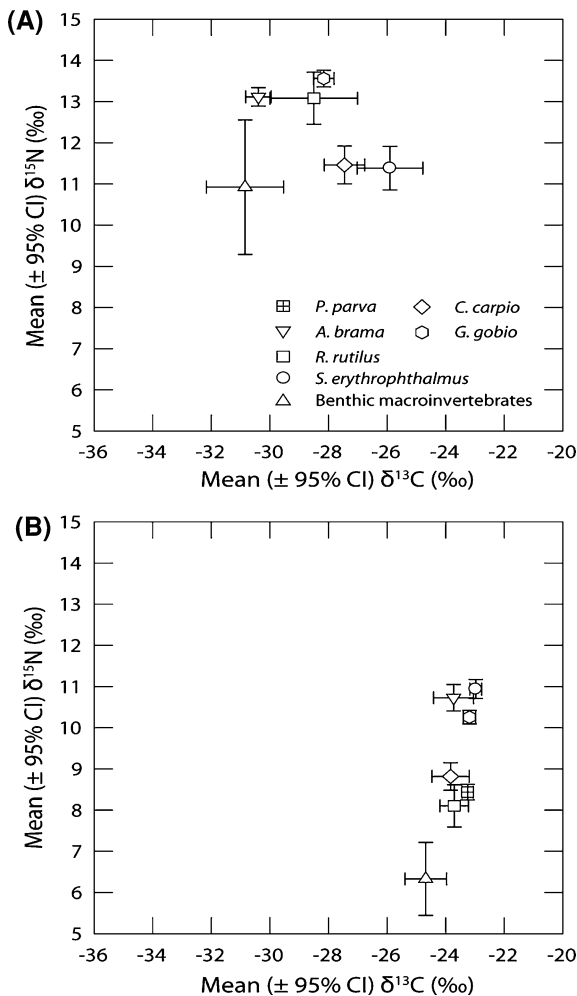
Fig. 2 Isotopic bi-plot showing variation in δ^{13}C and δ^{15}N for **a** the control pond and **b** the experimental pond. *Error bars* show 95% confidence limits

isotopic ratios estimated for putative macroinvertebrate prey (Fig. 2a; Table 3) indicated that species in the former group (*G. gobio, A. brama* and *R. rutilus*) may have had a more carnivorous diet than species in the latter group (*C. carpio* and *S. erythrophthalmus*).

The fish community from the experimental pond were far more ^{13}C enriched and ^{15}N depleted relative to the control pond (Fig. 2b; Table 2). Inter-specific variation in δ^{13}C was also less extreme, and only ranged between -23.8 (*C. carpio*) and $-23.0‰$ (*S. erythrophthalmus*). There was more variation in mean δ^{15}N values between species: *R. rutilus* were most ^{15}N depleted (8.1 ‰) whilst *S. erythrophthalmus* were most enriched (10.9 ‰). Examination of the

distribution of mean δ^{13}C and δ^{15}N values between the different fishes from the experimental pond again showed the existence of two putative groups. One group, consisting of *P parva, C. carpio* and *R. rutilus* was 2–3 ‰ depleted in δ^{15}N relative to the second group that included *A. brama, G. gobio* and *S. erythrophthalmus*. Both groups of fish were enriched in ^{13}C and ^{15}N relative to their putative macroinvertebrate prey (Fig. 2b; Table 2). Intra-specific (e.g. inter-pond) comparisons of mean δ^{13}C isotopic values were significant for all species, with individuals from the control pond being ^{13}C enriched relative to those from the adjacent, *P parva*-infested experimental pond (mean difference = 4.6 ‰: see Table 2 for *t*-tests). Mean δ^{15}N values were relatively enriched in the control pond (mean difference 3.3 ‰), with significant differences between *A. brama, C. carpio, G. gobio* and *R. rutilus* collected from the two ponds. However, the mean values of δ^{15}N values were similar in both ponds.

Comparison of δ^{13}C and δ^{15}N values from fishes collected from both ponds in a combined analysis (2-way MANOVA), and discounting *P. parva* as they were only present in the experimental pond, revealed a significant effect of both pond (Wilk's $\lambda = 0.379$, $F_{2,281} = 230.7$, $P < 0.001$) and species (Wilk's $\lambda = 0.613$, $F_{8,562} = 19.5$, $P < 0.001$). The significant interaction between these two terms (Wilk's $\lambda = 0.636$, $F_{8,562} = 17.8$, $P < 0.001$) revealed isotopic differences between the species were not consistent in each pond. A MANOVA comparing δ^{13}C and δ^{15}N values from the control pond suggested that the isotopic space inhabited by the five species was distinct (Wilk's $\lambda = 0.43$, $F_{8,290} = 19.06$, $P < 0.001$). Bonferroni-adjusted *post-hoc* GLM comparisons of mean canonical scores (from the first canonical function) revealed differing levels of overlap in the control pond. *A. brama* shared isotopic space with both *R. rutilus* ($P = 0.233$) and *S. erythrophthalmus* ($P = 0.177$). *C. carpio* only overlapped with *S. erythrophthalmus* ($P = 0.915$), whilst *G. gobio* only overlapped with *R. rutilus* ($P = 0.07$). A similar comparison of mean δ^{13}C and δ^{15}N values between the six species collected from the experimental pond was also significant (Wilk's $\lambda = 0.41$, $F_{10,370} = 20.6$, $P < 0.001$). As shown in the control pond, Bonferroni-adjusted *post-hoc* GLM comparisons of mean canonical scores revealed that the species inhabited different areas of δ^{13}C-δ^{15}N isotopic space. *A. brama* showed complete overlap with both

Table 2 Comparison of mean (±SD) δ^{13}C and δ^{15}N values in fish species collected from the control and experimental ponds

Species		δ^{13}C	Inter-pond			δ^{15}N	Inter-pond	
		Control	Experiment	t-test		Control	Experiment	t-test
Abramis brama	Mean	−30.4	−23.7	$t = 19.1$	Mean	13.1	10.7	$t = -13.94$
	SD	1.2	0.7	$df = 14.1$	SD	0.6	0.3	$df = 15.4$
	n	30	7	$P < 0.001$	n	30	7	$P < 0.001$
Cyprinus carpio	Mean	−27.5	−23.8	$t = 7.8$	Mean	11.5	8.8	$t = -9.5$
	SD	1.9	1.9	$df = 64.8$	SD	1.27	1.0	$df = 58.4$
	n	32	36	$P < 0.001$	n	32	36	$P < 0.001$
Gobio gobio	Mean	−28.2	−23.2	$t = 24.8$	Mean	13.6	10.3	$t = -26.2$
	SD	0.9	0.5	$df = 46.1$	SD	0.54	0.4	$df = 52.3$
	n	30	25	$P < 0.001$	n	30	25	$P < 0.001$
Rutilus rutilus	Mean	−28.5	−23.7	$t = 6.2$	Mean	13.1	8.1	$t = -12.4$
	SD	3.9	1.5	$df = 34.2$	SD	1.66	1.6	$df = 59.7$
	n	29	41	$P < 0.001$	n	29	41	$P < 0.001$
Scardinius erythrophthalmus	Mean	−25.9	−23.0	$t = 5.3$	Mean	11.4	10.9	$t = -0.45$
	SD	3	0.6	$df = 30.9$	SD	1.4	0.6	$df = 39.8$
	n	30	32	$P < 0.001$	n	30	32	$P = 0.121$
Pseudorasbora parva	Mean	–	−23.3	–	Mean	–	8.4	–
	SD	–	0.7	–	SD	–	0.7	–
	n	–	51	–	n	–	51	–

Note that in all cases (apart from *Scardinius erythrophthalmus* δ^{15}N), intra-specific comparisons showed large differences between the ponds

Table 3 Stable isotope ratio values for δ^{13}C and δ^{15}N for aggregated samples of macroinvertebrates collected from the control and experimental ponds

Taxon	Control δ^{13}C	Experimental δ^{13}C	Control δ^{15}N	Experimental δ^{15}N
Asselidae	–	−26.5	–	6.4
Baetidae	−29.0	−28.4	9.2	8.0
Caenidae	−30.5	−26.4	8.5	4.7
Chironomidae	−33.3	−27.3	11.0	5.4
Coenagriidae	–	−25.7	–	7.3
Dipteran larvae	–	−24.6	–	4.9
Gammaridae	−29.4	−24.2	13.7	8.4
Limnephilidae	−31.9	−27.7	11.6	4.4
Oligochaetae	–	−25.8	–	6.5
Platycnemididae	−31.1	−26.8	10.9	7.3
Polycentropidae	−31.2	–	12.4	–

G. gobio and *S. erythrophthalmus* ($P = 1.0$ in both cases). *G. gobio* also overlapped with *S. erythrophthalmus* ($P = 0.158$). *P. parva* overlapped with both *C. carpio* ($P = 0.26$) and *R. rutilus* ($P = 1.0$).

Thus, SIA revealed significant trophic overlap between *P. parva*, and *C. carpio* and *R. rutilus* in the experimental pond; this overlap shifted with individual size in these three species and was apparent across their entire length ranges (Fig. 3). In contrast, the δ^{15}N values of *A. brama*, *S. erythrophthalmus* and *G. gobio* revealed their occupation of a higher trophic level than *P. parva* (Fig. 2) and in combination with δ^{13}C values, there is almost classical stepwise isotope enrichment to these fishes from the benthic macro-invertebrates and through to *P. parva*. This suggests in these species there was a shift in trophic position in the experimental
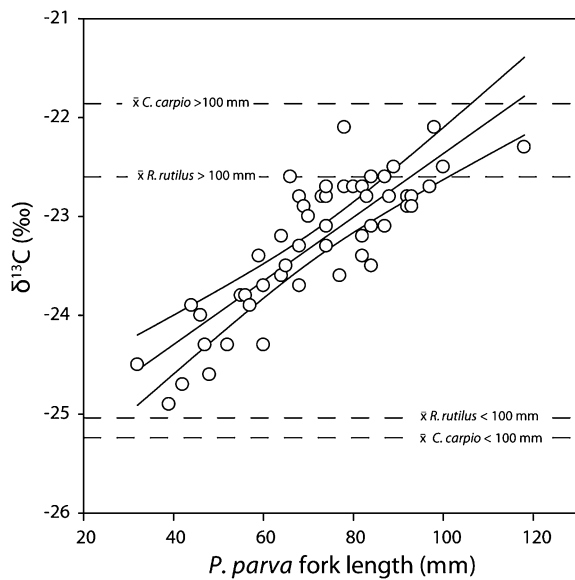
Fig. 3 Relationship of δ^{13}C and length (L_F) for *Pseudorasbora parva* in the experimental pond compared with mean δ^{13}C values for small *Rutilus rutilus* (70–100 mm), large *R. rutilus* (160–250 mm), small *Cyprinus carpio* (70–100 mm) and large *C. carpio* (250–500 mm)

pond as they may have actually been utilising *P. parva* as a food source.

Given the trophic overlap between *P. parva* and *R. rutilus*, but not *S. erythrophthalmus*, the somatic growth of these native species was compared between ponds in both pre- and post-*P. parva* invasion periods. Comparisons of mean length at age of *R. rutilus* between the ponds indicated fish in the experimental pond had reduced growth rates relative to those from the control pond (Fig. 4). Comparison of age-adjusted mean length (residuals of regression of length on age; 2-way ANOVA) showed no overall difference in mean back-calculated length at age between the two ponds ($F_{1,204} = 2.29$, $P = 0.131$), or between the pre- and post-invasion periods ($F_{1,204} = 2.49$, $P = 0.116$). However, a significant interaction between pond and invasion period ($F_{1,204} = 14.63$, $P < 0.001$) revealed clear differences in their growth in the two ponds following invasion (Fig. 4). Comparisons of mean age-adjusted length by Bonferroni post-hoc tests revealed that pre-invasion, their growth was the similar in both ponds ($P = 1.0$), was significantly reduced in the experimental pond post-invasion ($P = 0.001$), yet remained similar in the control pond in this period ($P = 0.747$).

Regarding somatic growth of *S. erythrophthalmus*, individuals in the experimental pond grew faster than those in the control pond (Fig. 4), with 2-way ANOVA of age-adjusted mean length (residuals of regression of length on age) revealing significant differences in mean back-calculated length at age between the two ponds ($F_{1,198} = 8.75$, $P = 0.003$), and between the pre- and post-invasion periods ($F_{1,198} = 18.14$, $P < 0.001$). The marked differences in *S. erythrophthalmus* growth between the two ponds and time periods were highlighted by a significant interaction between pond and invasion period ($F_{1,198} = 23.39$, $P < 0.001$). Comparison of their mean age-adjusted length by Bonferroni post-hoc tests (Fig. 4) revealed growth was similar in both ponds pre-invasion ($P = 1.0$). However, post-invasion, growth of *S. erythrophthalmus* in the experimental pond significantly increased ($P < 0.001$), but remained similar to the pre-invasion period in the control pond ($P = 1.0$).

Discussion

The rapid establishment of the numerically dominant *P. parva* population in the experimental pond resulted in significant trophic overlap between *P. parva* and all size classes of *R. rutilus*. This was subsequently associated with significantly depressed somatic growth in *R. rutilus*, a species common to freshwaters throughout much of Europe and western Eurasia. A shift in trophic position was also apparent in *S. erythrophthalmus* between the ponds; in the experimental pond, SIA values (δ^{15}N) indicated that they were assimilating energy at ca. one trophic level higher than in the control pond. In the experimental pond, the centroid of *S. erythrophthalmus* δ^{13}C-δ^{15}N isotopic space (δ^{15}N $\sim$ 3‰, δ^{13}C $\sim$ 1‰) was equivalent to a trophic level (Vander Zanden and Rasmussen 2001) above that of *P. parva*. This raises the question whether *S. erythrophthalmus* were actually consuming *P. parva*. The marked improvement in growth of *S. erythrophthalmus* following the invasion of *P. parva* indicates that feeding conditions certainly improved for this species. Further, there were significant differences in trophic position between the two ponds for all species present (except *P. parva*), suggesting invasion-mediated trophic shifts in the experimental pond and a possible shift in ecosystem

Fig. 4 Comparison of *Rutilus rutilus* (■, □) and *Scardinius erythrophthalmus* (○, ●) length (mm) at age (years) in the experimental (□, ○) and control pond (■, ●). Graphs **a**, **c**: back-calculated fork length at age of *R. rutilus* (**a**) and *S. erythrophthalmus* (**c**) in the two ponds. Graphs **b**, **d**: mean age-adjusted back-calculated length (residuals of length on age) between the two ponds in *R. rutilus* (**b**) and *S. erythrophthalmus* (**d**) pre- and post-invasion. *Lower case letters* adjacent to mean values indicate significant differences following Bonferroni post-hoc comparisons. *Error bars* show 95% confidence limits
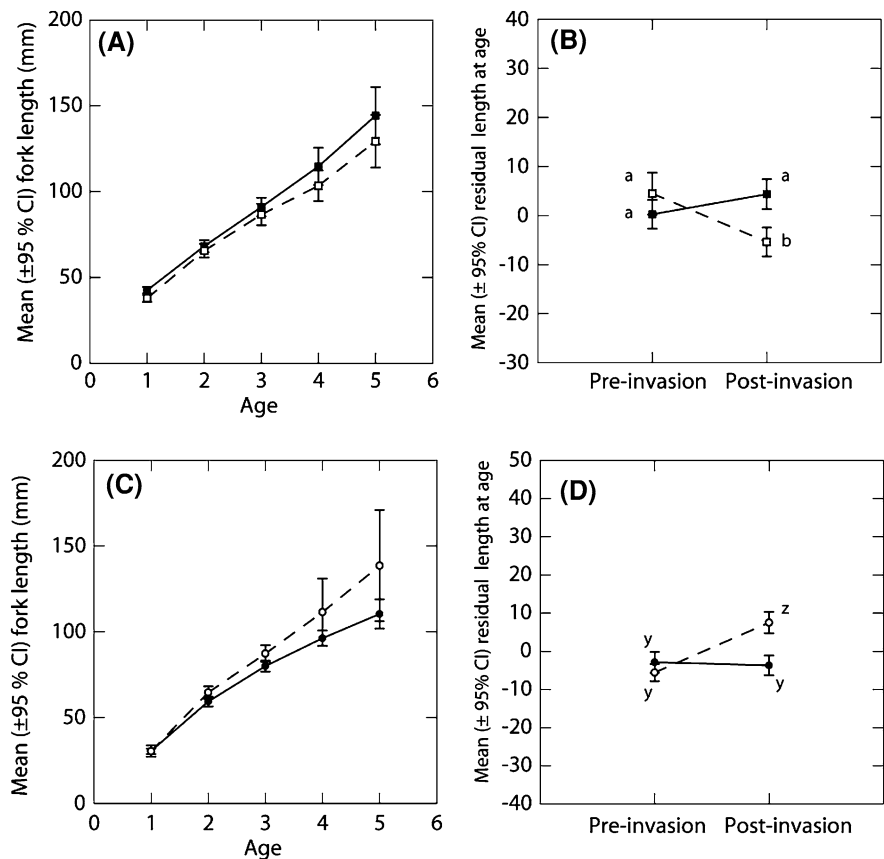
function (reduced mean trophic level). However, these had yet to impact at a community level between the ponds; with the exception of *P. parva* presence, the density and biomass of the fishes between the two ponds had remained broadly similar.

Taxa in the invaded pond generally showed enriched $\delta^{13}C$ and depleted $\delta^{15}N$ values relative to those from the control pond, indicating isotopic differences at the base of the foodweb. Furthermore, both fishes and their putative macroinvertebrate prey showed a very restricted range of $\delta^{13}C$ values, indicating that a single carbon source dominated the food web in the invaded pond (c.f. with the control pond, Fig. 2; Table 2). Due to the opportunistic nature of the study we have little information on the possible drivers (e.g. water chemistry, phytoplankton community structure) of the differences in isotopic baselines between the two ponds. However, possible explanations for the isotopic differences such as differential inputs of isotopically distinct C and N food sources (e.g. inputs of angling baits of marine origin or terrestrial-based vegetation) can be discounted.

Angling activities were similar on both ponds, and the addition of food to attract fish was restricted in both ponds. Both ponds had a similar amount of riparian vegetation, and as such are likely to have received similar amounts of ^{13}C-enriched terrestrial vegetation. Both ponds were turbid, with little scope for large inputs of benthic algae, which are typically ^{13}C enriched (France 1995). The relative ^{15}N depletion and ^{13}C enrichment in taxa from the invaded pond may reflect dominance by cyanobacteria of the phytoplankton community (Dokulil and Teubner 2000). Due to their ability to directly fix atmospheric nitrogen and utilise dissolved inorganic carbon, cyanobacteria are typically ^{15}N depleted and ^{13}C enriched relative to eukaryotic primary producers (Gu and Alexander 1993; Vuorio et al. 2006). The extreme densities of *P. parva* recorded in the invaded pond are likely to have exerted considerable grazing pressure on the zooplankton community (Hliwa et al. 2002). This would have resulted in a reduction in the mean size of zooplankton (Brooks and Dodson 1965), and therefore a limited capacity to graze large-bodied and

possibly unpalatable phytoplankton such as cyano-bacteria (Lynch and Shapiro 1981; Lampert 1987). As such, it is feasible that primary production in the invaded pond became dominated by cyanobacteria, leading to an overall ^{13}C enrichment and ^{15}N depletion in fish and other taxa. Grey et al. (2009) described isotopic shifts in fish and zooplankton from a shallow lake system similar to the differences between the two ponds, and associated these differences to changes in the phytoplankton community (i.e. loss of cyanobacteria) following biomanipulation.

Regarding the transferability of the study, it could be argued that the results of this study from two ponds of only 0.3 ha in area may not be representative of the wide range of *P. parva* invaded waters across Europe due to their variation from large lowland rivers to small floodplain lakes (e.g. Pollux and Korosi 2006). Notwithstanding, it is certainly the case that these ponds were highly representative of their invaded habitats in the UK. The majority of these are recreational lake fisheries of <1 ha and lack obligate piscivorous fish due to management interventions (Britton et al. 2007, 2008). Moreover, *R. rutilus* may be considered a ubiquitous fish of Europe and west Eurasia (Noble et al. 2007), and so their interaction with *P. parva* in this study may be representative of that experienced in similar, invaded waterbodies across the introduced range of *P. parva*. Regarding the robustness of the conclusions of the study, it could also be argued that these were hindered by the use of only one control pond with no replicates, a consequence of studying a natural system to quantify the ecological impact of this highly invasive fish. Whilst the outputs may have been even more robust through, for example, the complementary use of experimental enclosures, there is a strong ethical argument against using highly invasive fish in this manner. This is because any breach in biosecurity could result in their further dispersal, as has already occurred from a number of aquaculture sites in the UK (Pinder et al. 2005; Britton and Brazier 2006; Britton et al. 2008). Whilst there could have been a paucity of information on the pre-invasion status of the resident species, the use of back-calculated growth rates ensured that robust ecological comparisons were able to be made pre- and post-introduction, with the approach used in the study also recommended by Bøhn and Amundsen (2001). They argue that biologists increase the understanding of ecological interactions by following communities

during the establishment of exotic species. Through their study of the invasive vendace *Coregonus albula* (L.) over a 14-year period in a sub-arctic watercourse, they revealed the displacement of a native whitefish from its original niche by this invader, with a consequent >90% decline in population density (Bøhn et al. 2008). In studies such as these, whilst differences between the control and experiment systems are observed rather than tested, this should not make their outputs any less ecologically useful or significant.

In conclusion, this study quantified several ecological consequences of *P. parva* introduction on a fish assemblage; not only did they subsequently dominate the fish community, but their trophic overlap with resident fishes resulted in depressed growth rates (and so production) and shifts in trophic position. Thus, examination of the study's null hypothesis indicated it was only partially valid; through establishment of a sustainable population of *P. parva* and their integration into the foodweb, consequent trophic interactions did result in a measurable ecological impact on *R. rutilus* through depressed somatic growth, although this had not been concomitant with a change at the level of community composition. As these outputs revealed a negative ecological consequence of *P. parva* introduction and establishment, they can be used to better inform and refine existing risk assessment protocols and management decision-making tools for this highly invasive species.

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