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PRIMARY RESEARCH PAPER

Do non-native pumpkinseed *Lepomis gibbosus* affect the growth, diet and trophic niche breadth of native brown trout *Salmo trutta*?

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Abstract Brown trout *Salmo trutta* Linnaeus, 1758, is a priority species for conservation and management efforts in many European countries. In its native range, interactions with non-native fishes often adversely affect somatic growth rates and population abundances. Consequences of introduced North American pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758) for native *S. trutta* were examined in stream stretches with and without *L. gibbosus*. Data for somatic growth rates and trophic niche breadth (using stable isotope analyses) provided little evidence of *L. gibbosus* presence being detrimental for *S. trutta*. Shifts in *S. trutta* diet at all sites were associated with increased piscivory with increasing body length, with no evidence to suggest that interspecific resource competition with *L. gibbosus* structured the food web or affected trophic positions. Three years later, and following *L. gibbosus* removal, data revealed slight shifts in the food web at each site, but these related to shifts in resources at the bottom of the food chain rather than a response to *L. gibbosus* removal. Consequently, the ecological consequences of

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L. gibbosus for *S. trutta* in the study stream were minimal, with *S. trutta* populations responding more to natural mechanisms regulating their populations than to the presence of this non-native fish species.

Keywords Stable isotope analysis · Alien species · Environmental impacts · Introduced species · Circular statistics · Ecological consequences · Small streams

Introduction

Freshwater ecosystems often have high rates of introductions of non-native fishes arising from both intentional and accidental releases of species that are associated with, for example, fishery enhancement and the release of unwanted ornamental and bait fishes (Cohen & Carlton, 1998; Copp et al., 2005; Winfield et al., 2011; Jackson & Grey, 2013). Problems potentially occur when these fish integrate into the community, interact with native species, and increase competition for resources that instigate cascades that result in community- and ecosystem-level impacts (Cucherousset & Olden, 2011). Indeed, introduced fishes have been shown to alter food-web structure through increased competition for resources (Vander Zanden et al., 1999; Britton et al., 2010a), which disrupts natural habitat integrity via direct trophic links (Witte et al., 1992). However, these impacts are highly context dependent, and the extent to which these potential ecological consequences are realised is at least partially influenced by the biological and ecological traits of both the native and introduced fishes (Jackson et al., 2015; Paterson et al., 2015).

Brown trout *Salmo trutta* Linnaeus, 1758, is widely distributed across Europe and their populations are of high ecological, recreational and commercial value. Consequently, *S. trutta* has priority status in areas of its native range (Piccolo, 2011; Filipe et al., 2013), including high conservation designation (e.g. JNCC, 2014). Despite their value and conservation status, native *S. trutta* populations have been exposed to a number of non-native species across their European range with varying outcomes. For example, when in sympatry with introduced brook trout *Salvelinus fontinalis* (Mitchill, 1814), high dietary overlap occurs (Cucherousset et al., 2007) potentially resulting in reduced *S. trutta* somatic growth rates (Korsu et al., 2009). In those parts of Europe where European minnow *Phoxinus phoxinus* (Linnaeus, 1758) has been introduced and become invasive, competition for food resources with *S. trutta* can result in substantial reductions in *S. trutta* population abundances and somatic growth rates (Museth et al., 2007, 2010; Borgstrøm et al., 2010). By contrast, when exposed to non-indigenous amphipods, population abundances of *S. trutta* can increase via enhanced food availability (Kelly & Dick, 2005). This emphasises that the consequences of invasions for *S. trutta* depend upon local factors such as the specific invading species and the structural and functional character of the invaded ecosystem.

The North American centrarchid, pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758), is a small-bodied, warm-water fish that was introduced into Europe in the late 19th Century for both ornamental and sport fishing purposes, with populations now established in at least 28 countries across Eurasia (Copp & Fox, 2007). An omnivorous species (García-Berthou & Moreno-Amich, 2000), *L. gibbosus* inhabits both lentic and lotic environments but most studies have been on pond-dwelling populations (e.g. Copp et al. 2002; Villeneuve et al., 2005; Fox et al., 2011), although studies of stream-dwelling populations also exist (Cucherousset et al., 2009; Fobert et al., 2013; Almeida et al., 2014). Investigations of stream-dwelling populations in England have focused on the expression of their life-history traits, habitat use and dispersal (Stakėnas et al., 2009; Vilizzi et al., 2012; Fobert et al., 2013), with recent research in Iberia examining interspecific aggression (Almeida et al., 2014). Thus, there is limited information on their feeding interactions with, and consequences for, native fishes such as *S. trutta*. Initial habitat studies in two tributaries of the River Ouse (Sussex, England) suggested a potential association (or interaction) between native *S. trutta* and non-native *L. gibbosus* (Klaar et al., 2004). Subsequent telemetry studies at the microhabitat scale revealed the two species to exploit different parts of pools (Vilizzi et al., 2012), the preferred stream mesohabitats of both species (Stakėnas et al., 2013). Despite this repartition of spatial resources, there remains a potential adverse

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impact on the growth or trophic position of *S. trutta* from invasions of smaller-bodied fishes (Borgstrøm et al., 2010; Museth et al., 2010). Therefore, the aim of the present study was to assess the consequences of introduced *L. gibbosus* for *S. trutta* somatic growth rates, diet and trophic relationships and discuss their conservation implications.

Materials and methods

Study sites and sample collection

The study sites were in Batts Bridge Stream, a small tributary of the Sussex Ouse in Southern England that passes through a number of small, man-made in-stream reservoirs before its confluence with the main river (Copp et al., 2010). There is no evidence to suggest *L. gibbosus* breed in the Sussex Ouse catchment (Villeneuve et al., 2005; Copp et al., 2010), and their presence in Batts Stream has been shown (Fobert et al., 2013) to result from escapees from established *L. gibbosus* populations in floodplain ponds and in-stream reservoirs (Klaar et al., 2004; Copp & Fox, 2007). This dispersal into the stream system is associated with extreme flood/spate events (Fobert et al., 2013), with the stream-dwelling *L. gibbosus* achieving up to seven years of age, elevated lengths at maturity and low gonado-somatic index values (Villeneuve et al., 2005). The present trophic study took place at three stream sites (all three of 200 m length) in July 2007, two stretches in which *S. trutta* and *L. gibbosus* were sympatric in high (site A) and low (site B) densities and a third (site C) where the species was not observed during any of several surveys between August 2001 (Klaar et al., 2004) and July 2010 (Copp et al., 2010) except a single specimen in November 2004. Under the UK's 'The Prohibition of Keeping or Release of Live Fish (Specified Species) Order 1998', it is illegal to return regulated fish species to open waters. Therefore, with the exception of studies involving fish tagging techniques for which derogations were received (i.e. Fobert et al., 2013; Stakėnas et al., 2013), all *L. gibbosus* captured during surveys prior to 2010 were retained for laboratory analysis. This constituted an on-going removal programme, with successful extirpation of *L. gibbosus* from the stream assumed to have taken place in July 2007 because *L. gibbosus* was not captured at any of the sites after that survey, including the single-run survey of site A in October 2009 (Table 1). For the present study, additional data for stable isotope analysis were collected in July 2010 from all sites to match those collected in July 2007.

Fish sampling in July 2007 and 2010 was undertaken using a back-pack electrofishing unit (Bretschneider EFGI 650, Reichenbrnder Strasse 4, D-09224 Chemnitz/Gruna, Germany) whilst moving slowly in an upstream direction. A multiple-run strategy provided depletion estimates (three runs, depending on the depletion rate) that ensured thorough sampling to confirm the absence of *L. gibbosus* in site C from July 2007 and at all sites from October 2007 onwards. Following their capture, all fish were anaesthetised (MS-222), identified to species level, measured for total length (L_T; nearest mm), and a pelvic fin clip (*L. gibbosus* and *S. trutta*) and scale sample taken (*S. trutta* only). All procedures were completed under UK Home Office licencing. Upon recovery, and at the conclusion of the sampling, all fish were returned to the river alive except *L. gibbosus* due to their regulation as a non-native species under UK law (cited here above). On the same dates, samples of macro-invertebrates and terrestrial basal resources (grasses and leaves) were also collected.

Somatic growth rates

The *S. trutta* scales were aged on a projecting microscope (×48 magnification). To minimise errors in age estimation, a quality control procedure was utilised as per Musk et al. (2006), and all scales were viewed for an individual fish prior to its age determination. Agreement in ages during the quality control procedure was always above 90%. Following age determination, fish L_T at age was determined for each specimen by back-calculation (scale proportional technique; Francis, 1990), before calculation and testing of the mean standardised growth residuals for each site using two methods (Jones, 2000; Benstead et al., 2007; Storm and Angilletta, 2007) that tested the effect on life-time growth (method 1) and juvenile growth (method 2). To avoid statistical complications from using repeated measurements from individual fish in the same test (i.e. pseudo-replication), in both methods only one L_T per fish was used in each test (Britton et al., 2010a; Beardsley & Britton, 2012). Method 1 used the back-calculated L_T at the last annulus from each fish,

Table 1 Density (fish 100 m^{-2}) based on data from three depletions in all surveys except in 2009, which was a single pass (*), whereby the total number of fish captured in all depletions was standardised to the surface area of the stretch (i.e. stretch length × mean width derived from four measurements at the up- and downstream stop nets and at two transects at equal distances from the stop nets

Year	Site	*A. anguilla*	*C. gobio*	*G. gobio*	*L. gibbosus*	*L. planeri*	*P. fluviatilis*	*S. trutta*	Other
August 2001	A	0.7	0.6	7.8	8.5	0.7	0	7.8	0.3
August 2004	A	0	41.2	9.8	38.6	0	7.7	9.8	3.9
July 2007	A	0.6	6.3	34.7	14.8	2.6	0	4.5	0.6
October 2007	A	0.2	2.2	14.2	0	3.0	0	2.4	7.3
October 2009*	A	0.6	16.0	44.0	0	4.2	0	9.5	2.4
July 2010	A	0.2	4.5	25.4	0	1.2	0	7.9	0
August 2001	B	1.1	1.9	0.3	0.9	7.4	0	6.8	1.3
August 2004	B	0.3	17.2	5.7	0.6	0.6	4.6	4.3	0.6
July 2007	B	0.5	14.2	0.2	21.5	16.3	0.7	4.9	0
October 2007	B	0	2.8	0.0	0	8.9	0.0	8.4	0
July 2010	B	0	12.1	0.9	0	1.4	1.4	6.3	0.2
August 2001	C	0.4	36.1	1.6	0	0.2	0.2	7.4	2.2
August 2004	C	0.7	10.6	1.1	0.2	16.0	1.7	4.1	0.2
July 2007	C	0.6	71.6	0	0	11.9	1.5	6.7	0
October 2007	C	0.6	71.6	0	0	35.2	1.9	10.1	0.6
July 2010	C	0.6	26.2	0	0	3.8	0	5.2	0.8

The category 'Other' species includes infrequently encountered fishes: common bream *Abramis brama*, chub *Leuciscus cephalus*, goldfish *Carassius auratus*, European minnow *Phoxinus phoxinus*, northern pike *Esox lucius*, roach *Rutilus rutilus*, rudd *Scardinius erythrophthalmus*, stone loach *Barbatula barbatula* and rainbow trout *Oncorhynchus mykiss*. The values for 2001 and 2004 are derived from re-analysis of the raw data used in Klaar et al. (2004) and Copp et al. (2010)

using these to determine the mean L_T at each age for all sites using the log–log quadratic function of Vilizzi & Walker (1999), who identified this as the most precise and biologically meaningful growth model of five quadratic functions and the von Bertalanffy growth model. These values then enabled the standardised residual of the L_T at age of each fish at each site to be calculated (Britton et al., 2010a; Beardsley & Britton, 2012), with these then tested between the sites using ANOVA with Tukey's post hoc tests. Method 2 used a similar technique, except that the data tested were the back-calculated L_T at age 1 year for each fish, with their standardised residuals calculated from the mean L_T at age 1 for all sites. The effect of age at capture on L_T at age 1 was tested before differences in the standardised residuals between the sites were tested using ANOVA with Tukey's post hoc tests.

Stable isotope analysis

Fish diet composition and trophic niche breadth were quantified using the stable isotope analyses of carbon and nitrogen, as carbon isotopes reflect energy origin with typical enrichment of 0–1‰, whereas nitrogen isotopes indicate trophic position and show greater enrichment of 2–4‰ from resource to consumer (Post, 2002; Grey, 2006). All samples for stable isotope analysis (fish fin-clips, macro-invertebrates and terrestrial basal resources) were dried at 60°C for 48 h before being processed at the Stable Isotopes In Nature Laboratory (SINLAB). The stable isotope ratios were expressed as per mille (‰) using the delta notation (δ).

Differences in the stable isotope data and trophic niche of *L. gibbosus* and *S. trutta* were tested initially by quantifying the differences in $\delta^{13}C$ and $\delta^{15}N$ in July 2007 between the species using analyses of variance (ANOVAs). Variation in $\delta^{13}C$ and $\delta^{15}N$ of *S. trutta* between years was subsequently tested using analyses of covariance (ANCOVAs), with L_T as a covariate. The $\delta^{13}C$ and $\delta^{15}N$ values of both species were then used to calculate their standard ellipse areas (SEA_c), a bivariate estimate of the core isotopic trophic niche based on the distribution of individuals in the isotopic space (Jackson et al., 2011, 2012), for each year and site. This was completed using the SIAR package in R (R Core Team, 2013). The subscript 'c' indicates that a small sample size correction was used to increase the accuracy of the trophic niche estimate (Jackson et al., 2011). The extent to which the trophic niche overlapped in SEA_c between *L. gibbosus* and *S. trutta* at sites A and B in July 2007 was also quantified by calculating the bivariate area shared by both species in isotopic space and the proportion (%) of each species' core niche included in the shared area (Jackson et al., 2011, 2012).

To identify whether there was any consequence of *L. gibbosus* presence and absence (in July 2007 and July 2010, respectively) on food web structure at sites A and B, circular statistics (Wantzen et al., 2002; Schmidt et al., 2007) were performed (using Oriana 3.0; Rockware, Inc., Golden, Colorado, USA). In contrast to conventional statistical approaches, circular statistics allow the overall change in the bivariate isotopic composition (i.e. $\delta^{13}C$ and $\delta^{15}N$) of two groups to be calculated and tested for non-uniformity (Schmidt et al., 2007; Bartels et al., 2012). We grouped populations as four invertebrate functional groups (detritivores [Chironomidae, Ephemeridae], grazers [Plecoptera, Nemouridae], shredders [Gammaridae, Limnephilidae]) and filterers [Simuliidae]) and three native fish species (*S. trutta*, *Cottus gobio* Linnaeus, 1758, *Lampetra planeri* Bloch, 1784). The magnitude and direction (angle) of change in the isotopic composition of each group at each site were calculated between July 2007 (before removal) and July 2010 (after removal—i.e. the last of three consecutive surveys at site A that showed *L. gibbosus* to have been extirpated), using mean $\delta^{13}C$ and $\delta^{15}N$ values as coordinates (Batschelet, 1981; Schmidt et al., 2007). The magnitude of change was measured as the distance between the two points in $\delta^{13}C$ and $\delta^{15}N$ two-dimensional space, where the two points refer to the same population in July 2007 and in July 2010. The angle of change (from 0° to 360°) was then calculated as the clock-wise direction of this change in bivariate space. Rayleigh's test for circular uniformity assessed whether the directional change departed non-randomly from uniformity at each site (i.e. whether mean angular change in the isotopic composition of stream populations between July 2007 and July 2010 was non-random; Batschelet, 1981; Schmidt et al., 2007). If non-uniformity was detected, then a Watson–Williams test was used to test for differences in directional change between sites.

Results

Abundance, lengths and somatic growth rates

L. gibbosus were only present at sites A and B until July 2007 (Table 1), whereas *S. trutta* was present at all three sites in both years and in higher densities at sites A and B in July 2010 relative to July 2007 (Table 1). Maximum L_T of *S. trutta* remained largely unchanged at all three sites (Table 2), but the minimum L_T at capture in July 2010 was lower at the two sites (A, B), where *L. gibbosus* were present in July 2007 but no longer in 2010. Age data from July 2007 revealed that the maximum estimated age of *S. trutta* was 3 + years at site A and 4 + years at site B and C. There were no significant differences in the life-time growth of *S. trutta* between any of the sites in the July 2007 samples ($F_{2,92} = 0.34$, $P > 0.05$; mean difference ± SE; A–B: 0.22 ± 0.28, $P > 0.05$; A–C: 0.13 ± 0.28, $P > 0.05$; B–C: 0.10 ± 0.28, $P > 0.05$). For their L_T at age 1 (i.e. juvenile growth), there was no relationship between age at capture and L_T at age 1 (linear regression: $r^2 = 0.01$; $F_{1,93} = 0.69$, $P > 0.05$) and so age at capture was not used as a covariate in subsequent tests. These revealed that there were also no significant differences between juvenile

Table 2 Minimum and maximum of fish total length (L_T, in mm) and standard ellipse areas (SEA_c) for *Salmo trutta* and *Lepomis gibbosus* at each study stretch in July 2007 and July 2010. Number in parentheses indicates the number of individuals analysed for stable isotopes

Site	Population	Year	L_T (min–max)	SEA_c (‰^{2})
A	*S. trutta*	2007	49–311	5.4 ($n = 32$)
		2010	34–303	4.01 ($n = 27$)
	L. gibbosus	2007	43–121	1.67 ($n = 44$)
		2010	–	–
B	*S. trutta*	2007	70–289	4.53 ($n = 55$)
		2010	36–286	7.42 ($n = 27$)
	L. gibbosus	2007	52–134	3.01 ($n = 51$)
		2010	–	–
C	*S. trutta*	2007	48–335	3.29 ($n = 45$)
		2010	45–320	4.18 ($n = 25$)

growth of *S. trutta* at any of the sites in the July 2007 samples ($F_{2,92} = 2.06$, $P > 0.05$; mean difference ± SE; A–B: 0.31 ± 0.38, $P = 0.06$; A–C: 0.16 ± 0.18, $P > 0.05$; B–C: 0.15 ± 0.21, $P > 0.05$.

Trophic ecology

In July 2007, the δ^{15}N and δ^{13}C values of *L. gibbosus* (Fig. 2) were significantly different from *S. trutta* in sites A and B (site A, δ^{15}N: $F_{1,74} = 22.62$, $P < 0.001$; δ^{13}C: $F_{1,74} = 4.76$, $P = 0.03$; site B, δ^{15}N: $F_{1,104} = 75.10$; $P < 0.001$, δ^{13}C: $F_{1,104} = 77.69$, $P < 0.001$). The trophic niche breadth (SEA$_c$) of *L. gibbosus* overlapped that of *S. trutta* by 4.7% (site A) and 0% (site B) in July 2007, with *S. trutta* occupying a larger trophic niche than *L. gibbosus* (Fig. 1; Table 2). In July 2007, the δ^{13}C of *S. trutta* increased significantly with L_T at sites A ($F_{1,55} = 139.6$, $P < 0.001$), B ($F_{1,78} = 104.6$, $P < 0.001$) and C ($F_{1,66} = 157.1$, $P < 0.001$), with this also apparent in 2010 (A, $F_{1,55} = 0.72$, $P = 0.4$; B, $F_{1,78} = 0.07$, $P = 0.79$; C, $F_{1,66} = 3.09$, $P = 0.08$; Fig. 2). This indicates an ontogenetic diet towards discovery since fish resources had higher carbon signatures than invertebrate resources across all sites (Table 3).

The shift in each stream community's isotopic composition (and therefore food web structure) between July 2007 and July 2010 did not differ significantly among the sites (Fig. 3) and did not vary from uniformity (Rayleigh tests: $P > 0.05$), with the exception of site A (Rayleigh test: $P = 0.02$). The shifts in basal resource (tree leaves) and stream population (invertebrates, fish) isotope signatures at site A were in the same direction (i.e. carbon depletion; Tables 2, 3), indicating the observed directional change at site A resulted from a natural isotopic shift in basal resources, rather than being related to the removal of *L. gibbosus*.

Discussion

Empirical evidence indicates that non-native fishes can have damaging consequences for native fishes and communities as a result of trophic interactions (Baxter et al., 2004; Munawar et al., 2005, Cucherousset & Olden, 2011), including native populations of *S. trutta* (Museth et al., 2007, 2010; Borgstrøm et al., 2010). The present study, however, suggests that there were minimal influences of non-native *L. gibbosus* on native *S. trutta* somatic growth rates (juvenile and life-time) and trophic position in a stream in Southern England. Although the study had low replication, using only two invaded sites and one un-invaded site, these outputs were supported by the results obtained following the removal of *L. gibbous* and by data from previous studies of habitat use in which *S. trutta* and *L. gibbosus* in the upstream stretch (site A) of the stream were found to occupy different parts of (i.e. microhabitat repartition) the pool mesohabitats preferred by both species (Vilizzi et al., 2012; Stakėnas et al., 2013). In combination, these outputs indicate patterns of both habitat and resource partitioning between the species. Consequently, from a conservation perspective, our results suggest minimal impact by non-native *L. gibbosus* on the population status of *S. trutta* in streams in Southern England, and as such there is currently little requirement for subsequent management actions to minimise their ecological interactions. However, recent studies in the same stream system have demonstrated that extreme hydrological events (floods, spates), such as predicted for future climatic conditions (Jenkins et al., 2009), could enable *L. gibbosus* to establish new pond populations readily (Fobert et al., 2013).

Stable isotope analysis is a popular tool in invasion studies (e.g. Jackson et al., 2012; Sagouis et al., 2015), and here we have shown that it can be valuable in predicting whether or not an invader of stream ecosystems will impact co-existing natives. We found that there was negligible niche overlap between *S. trutta* and *L. gibbosus*, with no change in *S. trutta* growth in the presence and absence of the invader, which indicates that stable isotope estimates of niche overlap can be used to predict potential competition and impacts. We also found that the *S. trutta* populations had a larger dietary breadth than *L. gibbosus* through their significant ontogenetic trophic shift, which resulted in increased piscivory with increasing body size. That this was related to ontogeny and evident in all sites and in the presence and absence of *L. gibbosus* was important, as other studies have suggested that natural ontogenetic diet shifts in native fishes can change following the introduction of an invasive species. For example, the invasion by common carp *Cyprinus carpio* Linnaeus (1758) was indirectly responsible for the gradual decline of size-structured diet in largemouth bass *Micropterus salmoides* (Lacepède, 1802) in Lake Naivasha, Kenya,

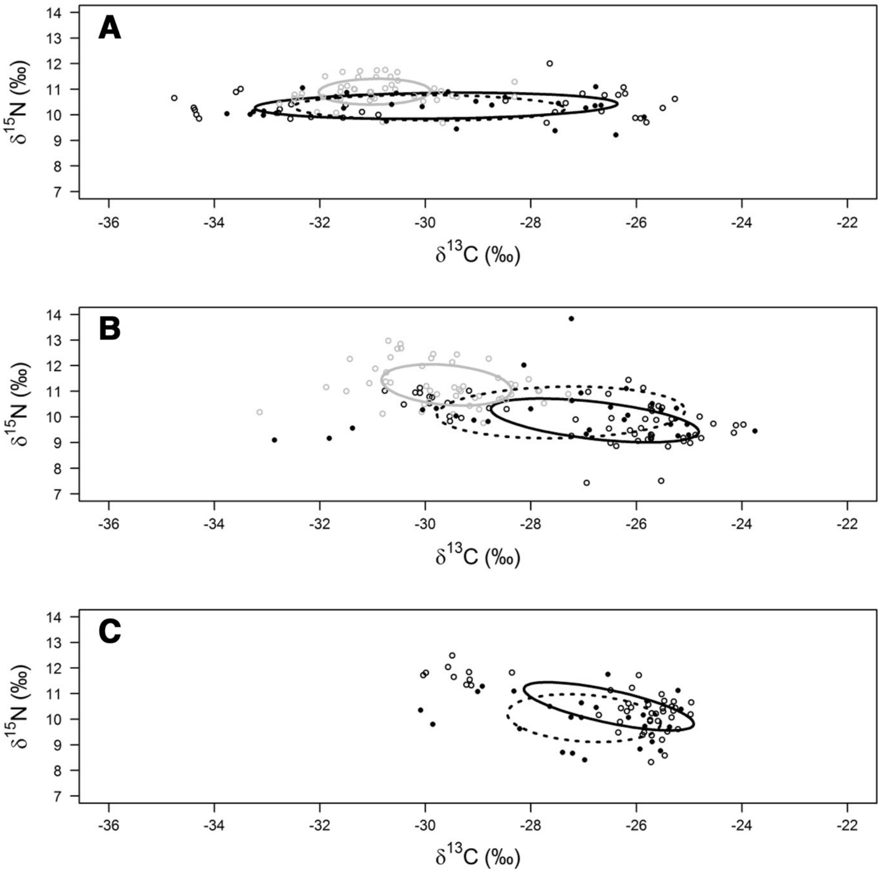
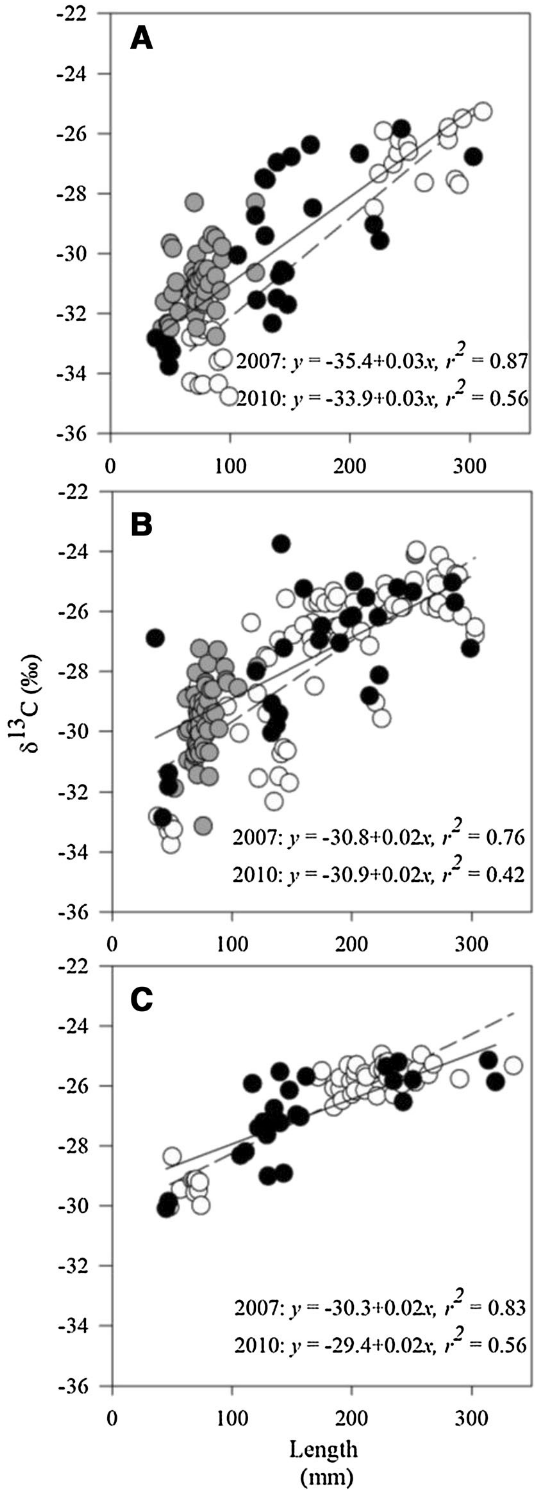


Fig. 1 Stable isotope values ($\delta^{15}N$ and $\delta^{13}C$ in ‰) of *Salmo trutta* (*black*) and *Lepomis gibbosus* (*grey*) at sites **A**, **B** and **C**. Data points represent individual fish sampled in July 2007 (*open circles*) and July 2010 (*closed circles*). Ellipses represent the standard ellipse area of each population in July 2007 (*solid lines*) and July 2010 (*dashed lines*)

because of its impact on water clarity (Britton et al., 2010b). Such changes were not, however, detected in the present study and this may relate to the fact that *L. gibbosus* currently is not currently invasive in England (Cucherousset et al., 2009) and, as such, their presence might not be sufficient to exert a long-term shift in stream community structure. Invasive species differ from non-native species by having an impact on the recipient ecosystem, which currently has not been demonstrated for *L. gibbosus* in England. This conclusion is supported by our food-web results, which also indicated minimal ecological consequences arising from *L. gibbosus* presence. Instead, shifts in the food web between July 2007 and July 2010 resulted from shifts in the baseline resources that were independent of *L. gibbosus* presence or absence.

In other parts of its European range, such as Spain and Portugal (Godinho et al., 1997), evidence suggests that *L. gibbosus* is mainly invasive in disturbed, lentic parts of river systems (Mesquita et al., 2006; Almeida et al., 2009), where it can impact on community structure (Angeler et al., 2002; Prenda-Marin et al., 2003). Similarly, in the Netherlands, in ponds invaded by *L. gibbosus*, impacts on the composition of macro-invertebrate assemblages have also been reported (Van Kleef et al., 2008); however, the *L. gibbosus* invasion of these ponds followed intensive rehabilitation work (dredging) to favour native plant species, so the invader was again benefiting from environmental disturbance (Ross, 1991; Almeida et al., 2009). That such impacts were not detected in the present study may be for two reasons. Firstly, *L. gibbosus* has yet to establish self-sustaining populations in U.K. water courses (Cucherousset et al., 2009), which contrasts to Southern Europe, where invasive populations inhabit both lotic and lentic environments and in both cases they are characterised by faster juvenile growth and earlier maturity, thus enhancing recruitment and as a consequence the potential for detrimental effects on the surrounding ecosystem (Fox et al., 2007). Whilst currently non-



◀**Fig. 2** Relationship between total length (mm, *grey*: *Lepomis gibbosus*, *white*: *Salmo trutta* in July 2007 and *black*: *S. trutta* in July 2010) and δ^{13}C at sites **A**, **B** and **C**. *Regression lines* are shown for trout in 2007 (*dashed*) and 2010 (*solid*)

invasive in the U.K., *L. gibbosus* has been predicted to benefit from warmer future temperatures predicted under conditions of climate change (Britton et al., 2010c), with likely increases in dispersal via fluvial environments (Fobert et al., 2013), and this has been supported by field-based experiments of spawning and recruitment (Zięba et al., 2010; Zięba et al., 2015). Further, with increasing temperatures, which are closer to the optimum of *L. gibbosus*, their impact on the recipient community is likely to be more pronounced (Rahel and Olden, 2008). Thus, the negligible impact recorded in the present study might change in future scenarios. Secondly, most of the documented negative effects of *L. gibbosus* in its invasive range in Europe has been in lentic systems (Cucherousset et al., 2009), with only one recent in situ stream study, which revealed adverse (aggressive) impacts by *L. gibbosus* on native fishes (Almeida et al., 2014)—this contrasts our study system in which habitat and resource partitioning is more apparent (Vilizzi et al., 2012; Stakėnas et al., 2013). We suggest that similar negative ecological consequences, as observed in Iberia and the Netherlands, may be discovered in future studies of ponds invaded by *L. gibbosus* in England, as that is where the densest populations of *L. gibbosus* are found in the U.K. (Fox et al., 2011), especially where these have been recently disturbed (Ross, 1991; Van Kleef et al., 2008).

There is a preponderance of literature in which adverse ecological impacts on native species, including *S. trutta* (Museth et al., 2007, 2010; Borgstrøm et al., 2010), are attributed to non-native fishes (Vitule et al., 2009; Gozlan et al., 2010; Cucherousset & Olden 2011) due to increased predation and/or competition, habitat modifications and interactions resulting in interference, e.g. hybridisation, aggression (García-Berthou 2007; Gozlan et al., 2010; Cucherousset & Olden 2011; Almeida et al., 2014). It is therefore important to report on cases where the effects of a non-native fishes are negligible or at least relatively benign (e.g. Fobert et al., 2011), especially in relation to prioritising the non-native species for management actions (Britton et al., 2011). Moreover, Hansen et al. (2013) suggest that there are generally few differences between the abundances of non-native and native species within invaded habitats, with ecological impacts often associated with species-specific relationships between abundance and impact

Table 3 Mean stable isotope values (±SE; *n* given in Table 2) of *Lepomis gibbosus* and the three *Salmo trutta* size classes (*S tr*), as well as the resources ($n = 3$–6 for each) per site and per year, including *Cottus gobio* and *Lampetra planeri*

Site	Species/ resource	July 2007		July 2010	
		δ^{15}N (‰)	δ^{13}C (‰)	δ^{15}N (‰)	δ^{13}C (‰)
A	*L. gibbosus*	10.9 ± 0.10	−30.97 ± 0.16	–	–
	Small *S tr*	10.2 ± 0.10	−33.0 ± 0.32	10.1 ± 0.00	−3.6 ± 0.10
	Medium *S tr*	–	–	10.3 ± 0.10	−29.7 ± 0.50
	Large *S tr*	10.5 ± 0.10	−26.60 ± 0.23	10.6 ± 0.20	−27.9 ± 0.70
	C. gobio	11.6 ± 0.60	−30.1 ± 0.40	12.1 ± 0.09	−30.9 ± 0.20
	L. planeri	6.5 ± 0.20	−27.3 ± 0.40	6.9 ± 0.20	−29.9 ± 0.50
	Detritivore	7.9 ± 1.00	−31.4 ± 1.10	8.8 ± 0.60	−33.6 ± 0.20
	Filterer	8.5 ± 0.04	−35.6 ± 0.20	7.8 ± 0.10	−36.0 ± 0.10
	Grazer	7.1 ± 0.40	−33.0 ± 0.01	8.1 ± 0.60	−34.6 ± 0.70
	Shredder	6.7 ± 0.20	−31.6 ± 0.30	7.2 ± 0.10	−31.7 ± 0.50
	Grass	0.2 ± 0.20	−33.7 ± 0.10	–0.8 ± 0.10	−33.0 ± 0.10
	Tree leaf	0.08 ± 0.4	−28.7 ± 0.80	–0.8 ± 0.04	−31.7 ± 0.50
B	*L. gibbosus*	10.9 ± 0.10	−31.0 ± 0.20	–	–
	Small *S tr*	10.6 ± 0.10	−29.7 ± 0.20	9.3 ± 0.10	−31.1 ± 1.30
	Medium *S tr*	9.4 ± 0.30	−26.1 ± 0.20	10.1 ± 0.10	−27.0 ± 0.60
	Large *S tr*	9.7 ± 0.10	−25.4 ± 0.20	10.5 ± 0.40	−26.5 ± 0.40
	C. gobio	11.4 ± 0.04	−29.7 ± 0.50	10.9 ± 0.30	−29.7 ± 1.00
	L. planeri	7.4 ± 0.50	−28.1 ± 0.10	7.3 ± 0.04	−27.01 ± 0.20
	Detritivore	9.7 ± 0.01	−32.6 ± 0.01	8.1 ± 0.70	−31.4 ± 1.00
	Filterer	6.3 ± 0.01	−37.0 ± 0.01	6.9 ± 0.03	−31.9 ± 0.20
	Grazer	8.1 ± 0.10	−32.2 ± 0.20	6.6 ± 0.20	−37.4 ± 0.70
	Shredder	6.7 ± 0.10	−30.2 ± 0.10	5.8 ± 0.20	−29.8 ± 0.60
	Grass	1.2 ± 0.70	−32.2 ± 0.80	3.5 ± 0.10	−33.5 ± 0.01
	Tree leaf	–0.1 ± 0.4	−28.3 ± 0.60	2.4 ± 0.1	−30.5 ± 0.03
C	*L. gibbosus*	–	–	–	–
	Small *S tr*	11.8 ± 0.11	−29.4 ± 0.20	10.1 ± 0.30	−30.3 ± 0.10
	Medium *S tr*	10.2 ± 0.20	−26.0 ± 0.10	9.8 ± 0.20	−27.5 ± 0.30
	Large *S tr*	10.1 ± 0.10	−25.6 ± 0.10	10.5 ± 0.30	−25.9 ± 0.20
	C. gobio	10.8 ± 0.20	−28.2 ± 0.40	11.3 ± 0.20	−28.7 ± 0.40
	L. planeri	8.9 ± 0.20	−26.3 ± 0.40	7.1 ± 0.40	−25.4 ± 1.00
	Detritivore	9.2 ± 0.20	−29.2 ± 0.40	8.9 ± 0.20	−29.7 ± 0.01
	Filterer	8.8 ± 0.20	−30.9 ± 0.10	7.7 ± 0.04	−29.5 ± 0.00
	Grazer	11.1 ± 0.10	−29.5 ± 0.20	7.6 ± 0.10	−31.7 ± 0.40
	Shredder	7.7 ± 0.10	−27.6 ± 0.02	5.5 ± 0.30	−28.8 ± 0.40
	Grass	6.9 ± 0.10	−32.4 ± 0.20	1.8 ± 0.40	−30.7 ± 0.10
	Tree leaf	−1.2 ± 0.20	−28.7 ± 0.20	1.2 ± 0.03	−31.9 ± 0.10

(Jackson et al., 2015). Thus, as studies often focus on the ‘worst-case’ scenarios where high abundances of invaders result in high ecological impacts, this produces inherent bias within the literature, which potentially overstates the ecological consequences of non-native species per se (Gozlan, 2008). Consequently, although the present study had limitations in its extent of replication, and there were some inherent differences in body sizes between the fishes that could have been the driver of trophic and habitat partitioning (e.g. O’Farrel et al., 2014), it nevertheless provides a strong case study, which highlights an observed pattern that the consequences of non-native species on native species and communities are often relatively benign (Gozlan, 2008).

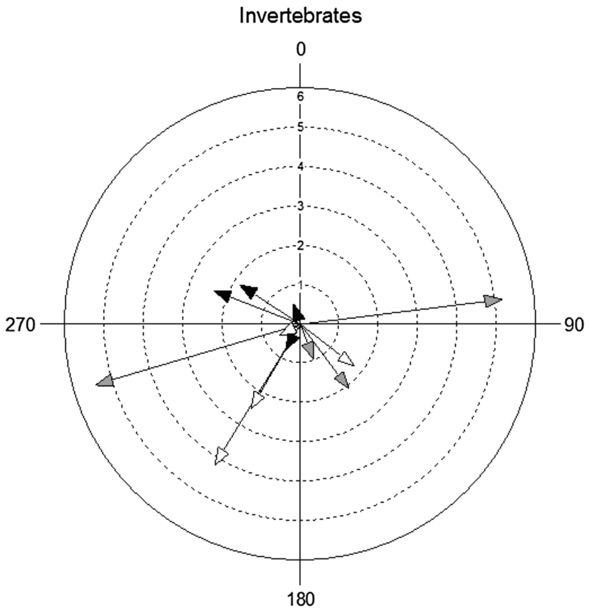


Fig. 3 *Arrow diagrams* showing the mean change in stable isotope values of invertebrate functional groups and fish between July 2007 and July 2010 at sites **A** (*black*), **B** (*grey*) and **C** (*white*). *Each arrow* represents a functional feeding group of invertebrates or species of fish and shows the direction and magnitude of change in their mean isotope signatures between years

Although we argue that the present study reveals that *L. gibbosus* is currently a benign non-native species in U.K. fluvial systems, it has already been outlined that the species' invasion status is not expected to remain static over the longer term. Their apparent invasive characteristics, which have been observed elsewhere in small, disturbed still waters (Van Kleef et al., 2008; Fox et al. 2011), are predicted to express themselves under conditions of climate warming (Britton et al., 2010c; Fobert et al., 2013; Zięba et al., 2015). Thus, whilst there was little evidence that non-native *L. gibbosus* had any ecological consequences for the native *S. trutta* populations of a stream in southern England, their spread to other systems (e.g. still waters) may have a more severe impact, especially under future scenarios of climate change.

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