RESEARCH ARTICLE

Novel trophic subsidies from recreational angling transform the trophic ecology of freshwater fishes

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Abstract

1. Angling is a globally popular leisure activity. There are over 31 million anglers in Europe, many of which target species of the Cyprinidae family in lowland freshwater ecosystems using methods generally involving bait (e.g. groundbaits, seeds and pellets), with large bait inputs possible in periods of high angling activity. While these bait inputs act as novel trophic subsidies ('angling subsidy'), substantial knowledge gaps remain on their influence on freshwater food webs, including on fish trophic niche size and position.

2. The effects of angling subsidies on the trophic ecology of cyprinid fish populations and their macroinvertebrate prey resources were investigated in field studies comparing waters of high angling activity ('subsidised fisheries') versus low angling activity ('non-subsidised fisheries'), and complemented by a pond experiment using two cyprinid species in subsidy absence/presence. Methods were based on stable isotope analysis, with angling subsidies being $\delta^{13}C$ enriched and, generally, $\delta^{15}N$ depleted compared to macroinvertebrate prey resources.

3. In the subsidised fisheries, while there were minimal influences of the baits on macroinvertebrate stable isotope values, the effects of the subsidies on all fish species were to substantially $\delta^{13}C$ enrich and $\delta^{15}N$ deplete their isotopic niches. However, patterns of interspecific niche divergence remained similar between the species in subsidy presence.

4. In the pond experiment, there was strong isotopic association between the two fish species and macroinvertebrate putative prey in subsidy absence. In treatments that then exposed both species to angling subsidies, their stable isotope values shifted to enriched $\delta^{13}C$.

5. *Synthesis and application.* Where angling activity is high, angling baits can provide strong trophic subsidies to freshwater fish, but with minimal effects on other trophic levels. Their regular input into freshwaters can provide some substantial benefits for fish (e.g. increased growth rates) and fisheries (e.g. elevated carrying capacity, higher catch rates), but can also increase nutrient enrichment and potentially raise concerns on angling ethics. Thus, in allowing the use of

these baits, especially in relatively high quantities, managers must balance the benefits they can deliver to fish and fisheries versus the adverse effects their use can have on freshwater organisms and ecosystem functioning.

1 | INTRODUCTION

Recreational angling is a highly popular leisure activity in which 10% of the global population participates (Arlinghaus & Cooke, 2009). There are over 31 million anglers in Europe (Arlinghaus et al., 2015), with many of these targeting species of the Cyprinidae family in lowland freshwaters (Amaral et al., 2013; Wolos et al., 1992). To capture these species, anglers use a range of different baits that they often release into freshwaters in relatively high quantities (Amaral et al., 2013; Arlinghaus & Mehner, 2003). For example, individual coarse anglers in Germany used an estimated 7.3 kg of bait per year, releasing an estimated total of 24,000 tonnes of bait in 2002 (Arlinghaus, 2004). Anglers that specialise on species such as carp *Cyprinus carpio* use, on average, 215 kg of bait per year (Niesar et al., 2004).

The baits used within angling for cyprinid fishes can be grouped into four general categories: seeds (mainly cereals, such as corn/maize), groundbaits (a mix of relatively fine plant and animal flours), boilies (boiled mix of animal or vegetable flours and eggs, formed into balls of up to 30 mm diameter) and pellets (pelletised animal flours and oils, often based on marine fishmeal, of diameters 1–32 mm; Imbert et al., 2022). In general, groundbaits are used for targeting smaller bodied cyprinid species (e.g. roach, *Rutilus rutilus*, and rudd, *Scardinius erythrophthalmus*), with boilies, pellets and seeds used for larger bodied species (e.g. carp, common bream, *Abramis brama*, European barbel, *Barbus barbus*) (Amat Trigo et al., 2017). Although the use of these baits is ubiquitous for targeting cyprinid fishes in lowland freshwaters, their release in high volumes is often on waters where the fish community has been modified by stocking activities that diversify the species present and/or increase the stock abundance (Cucherousset et al., 2021; Hickley & Chare, 2004).

The inputs of these angling baits into freshwater ecosystems potentially provide an important allochthonous trophic subsidy ('angling subsidy') that can substantially increase the fish production and carrying capacity of the system (Mehner et al., 2019). When released in even limited quantities, cyprinid fishes often consume them in preference to natural prey resources, reducing competition between trophically analogous species (Bašić & Britton, 2016). When these baits are released in high quantities over several days, carp learn the position of these feeding areas and exploit them repeatedly (Žák, 2021). In areas of high angling activity, larger bodied fish can specialise on these baits, with up to 80% of the diet of adult European barbel comprising of pelletised marine fishmeal in some English rivers (Bašić et al., 2015; De Santis et al., 2019; Gutmann

Roberts et al., 2017). However, there remains high uncertainty in the extent to which these angling subsidies affect the trophic ecology (e.g. trophic position, trophic niche size, individual specialisation) of fish and other freshwater taxa more generally, especially in relation to different levels of angling activity.

Angling baits can potentially be traced through freshwater food webs using stable isotope analyses (SIA) due to their isotopic differentiation with natural prey resources. For example, marine fishmeal baits have relatively enriched $\delta^{13}C$ values versus the relatively depleted $\delta^{13}C$ freshwater values of natural fish prey resources (Bašić et al., 2015; Grey et al., 2004). Corn and boilie baits are also strongly $\delta^{13}C$ enriched versus natural prey resources, with these differences enabling their diet contributions to be quantified after a 3-month exposure period in the cyprinid fishes (high contribution in some species) and macroinvertebrates (low contribution) of a German lake (Mehner et al., 2019). This isotopic differentiation between natural prey and angler baits means that when fish feed on these baits, it would be expected that their isotopic niche (analogous to the trophic niche; Jackson et al., 2012) would shift to enriched $\delta^{13}C$ (Bašić et al., 2015; De Santis et al., 2019). The extent of this $\delta^{13}C$ enrichment would be dependent upon the proportion of angling baits in their diet, with higher proportions resulting in greater shifts (Gutmann Roberts et al., 2017). Where the fish population comprises of individual specialists that consume high proportions of angler baits, with other individuals continuing to primarily consume natural prey, an increase in the size of the population isotopic niche would be expected as resource diversity is substantially increased (Bašić & Britton, 2016). This individual specialisation can also be modulated by fish body size due to the gape size limitation of smaller fishes (Sánchez-Hernández et al., 2019) and, therefore, higher individual dietary proportions of angling bait would be expected with increased body size (Gutmann Roberts et al., 2017). Given that patterns of partitioning in the trophic niches of fish species in the community are often strong (Britton et al., 2019; Jackson & Britton, 2014), then this partitioning is potentially disrupted if the fish populations shift their resource use towards mainly consuming angling baits.

The aim here was to assess how angling baits act as novel trophic subsidies and modify freshwater trophic ecology according to different levels of angling activity using a field study that was complemented by a pond experiment (Figure S1A). The field study used two qualitative categories of cyprinid angling activity: low activity ('non-subsidised fisheries') and high activity ('subsidised fisheries'). In the complementary pond experiment, fish diet was based only on natural prey resources for 3 years, followed by a year when an

angling subsidy was also available (Figure S1B). We posit that (a) angling baits are enriched in $\delta^{13}C$, with the stable isotope values of fish and their macroinvertebrate putative prey resources then also being $\delta^{13}C$ enriched in subsidy presence due to direct bait consumption; (b) fish trophic niches (as the isotopic niche) are then enriched in $\delta^{13}C$ in subsidy presence, resulting in strong patterns of niche convergence that are independent of fish length; and (c) the controlled release of an angler subsidy results in fish trophic niches shifting towards relatively enriched $\delta^{13}C$ values as fish consume the subsidy.

2 | MATERIALS AND METHODS

2.1 | Angling baits

A range of angling baits was sourced to determine their stable isotope values (as $\delta^{13}C$ and $\delta^{15}N$; see next section for their preparation and analysis), where the focus was on analysing pellets and groundbaits, but with dog biscuits also analysed given their observed use on some subsidised fisheries. Data on the stable isotope values of boilies and corn were available from Mehner et al. (2019).

2.2 | Field study

The subsidised fisheries comprised of six ponds and lakes used for catch-and-release recreational angling in southern England (2–20 ha in area, depths to 2 m). The exact locations of these sites cannot be provided to protect business confidentiality, as each was run as a private fishery. The fish community of all of these waters had been altered by stocking exercises involving carp (generally <5 kg), common bream, roach and rudd, although no stocking exercises has been completed for at least 2 years prior to sampling (Table S1A and S2). Direct observations of the extent of angling activity during sampling periods indicated relatively high activity with multiple anglers fishing, including in competitions of up to 5-hr duration, on a daily basis from May to October (e.g. up 20 anglers per hectare). These anglers were observed using a wide range of baits, including groundbait, corn and boilies, with pelletised fishmeal was always prominent. More quantitative estimates on angler numbers and bait inputs over time could not be determined for each site logistical constraints, including those imposed by Covid-19 restrictions at the time of sampling (summer 2020).

Fish were sampled between July and September 2020 by a combination of baited fish traps and rod and line angling during stock assessment exercises. Concomitantly, samples of putative macroinvertebrate prey resources (e.g. Gammaridae, Chironomidae) were collected using sweep netting and sediment grabs, with these sorted and then frozen prior to sample preparation. The sampled fish were identified (all were carp, common bream, roach and rudd), measured (fork length, FL, nearest mm) and scale samples taken (3–5 scales per fish). It was these scales that were used for stable isotope analysis, with scales tending to have a longer isotopic half-life than fin

tissue (Busst & Britton, 2018). The scales were not decalcified prior to isotope analysis, given that removal of inorganic carbonates has no significant effect on scale $\delta^{13}C$ and $\delta^{15}N$ values (e.g. Woodcock & Walther, 2014). Preparation was through cleaning with distilled water before removing the outer portion of the scale for SIA, ensuring the analysed tissue was from the most recent growth (Hutchinson & Trueman, 2006). Only one scale was analysed per individual fish as this provided sufficient material for analysis.

The non-subsidised fisheries comprised of nine freshwaters in which ecological studies had been completed by the lead author in the period 2013–2020. These sites were characterised by substantially lower angling activity, as observed directly by low angler activity during the study periods (from no anglers observed to <1 angler per hectare) and indirectly from relatively undisturbed riparian habitats (areas of high angling activity can result in localised vegetation loss and soil compaction; O'Toole et al., 2009) (Tables S1B and S2). These low levels of angling activity were then taken to represent low bait inputs too, with more quantitative estimates of angler numbers and bait inputs not being possible. To ensure that there were sufficient waters with the four cyprinid species present that were also in the subsidised fishery samples, these waters were a mix of ponds, lowland rivers and a canal (Tables S1B and S2). The lowland river sites were all relatively slow flowing reaches, including deep, impounded reaches between flow regulation and navigation weirs (S11, 13, 14; Tables S1B). Sampling used a combination of electric fishing and rod-and-line angling where, after their capture, fish were identified to species, measured (FL, nearest mm) and a scale sample collected for stable isotope analysis. Samples of fish putative macroinvertebrate prey resources had also been collected using sweep netting in all available habitats, sorting and then freezing prior to sample preparation.

All of the fish scale, macroinvertebrate and angling bait samples were then dried to constant mass at 60°C (sample sizes in Table S2) before analysis at the Cornell University Stable Isotope Laboratory (New York, USA) for $\delta^{13}C$ and $\delta^{15}N$ in a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific, USA) interfaced to a NC2500 elemental analyser (CE Elantach Inc., USA). Analytical precision of the $\delta^{13}C$ and $\delta^{15}N$ sample runs was estimated against an internal standard sample of animal (deer) material every 10 samples, with the overall standard deviation estimated at 0.08 and 0.04‰, respectively. Ratios of C:N indicated no requirement for lipid normalisation (generally 3.5–3.9) (Winter & Britton, 2021). To enable comparison of the SI data between the sites, the fish SI data were corrected (De Santis et al., 2021), where $\delta^{15}N$ data were converted to trophic position (TP) (Olsson et al., 2009):

$$TP = \left(\delta^{15}N_{fish} - \delta^{15}N_{prey} / 3.4\right) + 2,$$

where TP and $\delta^{15}N_{fish}$ are the trophic positions and the nitrogen ratios of each individual fish, $\delta^{15}N_{prey}$ is the mean nitrogen ratio of the putative macroinvertebrate prey resources (Table S3), 2 is the trophic position of these prey resources (as primary consumers) and 3.4 is the generally accepted fractionation factor between adjacent trophic levels

(Post, 2002). If the fish had been foraging on the putative macroinvertebrate prey groups used in the TP equation then the fish TP values would be expected to be between 2.5 and 4.5 (with variation resulting from differences in dietary proportions between individual fish) (Busst & Britton, 2016; Winter & Britton, 2021). Values outside of this range would indicate the consumption of alternative dietary items. The $\delta^{13}C$ data were converted to corrected carbon ($\delta^{13}C_{corr}$) (Olsson et al., 2009):

$$\delta^{13}C_{corr} = (\delta^{13}C_{fish} - \delta^{13}C_{meanMI}) / CR_{MI},$$

wherein $\delta^{13}C_{fish}$ is the $\delta^{13}C$ value of each fish, $\delta^{13}C_{meanMI}$ is the mean $\delta^{13}C$ of the macroinvertebrate prey and CR_{MI} is the carbon range ($\delta^{13}C_{max} - \delta^{13}C_{min}$) of the same macroinvertebrates (Olsson et al., 2009) (Table S3). As discrimination factors of $\delta^{13}C$ between prey and fish predators are generally 1–2‰, but can be higher for fin tissue (e.g. up to 4‰ on invertebrate based diets; Busst & Britton, 2016), then fish values of $\delta^{13}C_{corr}$ outside of these ranges (e.g. >4‰) would again suggest the fish were feeding on alternative dietary items.

Prior to further analyses, the $\delta^{13}C_{corr}$ and TP data from the non-subsidised fisheries were tested in generalised linear mixed effects models (GLMM) to check the validity of combining data over the three habitat types (pond/river/canal; Table S1B). In models, the dependent variable was $\delta^{13}C_{corr}$ or TP, fixed effects were habitat type, species and fish length, and site was a random effect. It was considered valid to combine the data for the non-subsidised fisheries if the effect of habitat type on $\delta^{13}C_{corr}$ and TP was not significant (cf. Section 3). GLMMs then tested differences in both $\delta^{13}C_{corr}$ and TP between the subsidised and non-subsidised fisheries, where the dependent variable was $\delta^{13}C_{corr}$ or TP, fixed effects were subsidy presence/absence, species, habitat type and fish length, and site was a random effect. Model outputs included mean values of $\delta^{13}C_{corr}$ and TP in subsidy presence/absence that were tested for the significance of their differences using pairwise comparisons (linearly independent, with Bonferroni correction for multiple comparisons).

The corrected data were then used to calculate the trophic niche sizes of each fish species in the subsidised and non-subsidies fisheries (combined data), and then per species and site (site-specific data) (Figure S1). These calculations used the isotopic niche as a proxy of the trophic niche (Jackson et al., 2011). While closely related to the trophic niche, the isotopic niche is also influenced by factors including growth rate and metabolism (Jackson et al., 2011). These niches were calculated using standard ellipse areas (SEA) in SIBER (Jackson et al., 2011, 2012), where SEAs are a bivariate measure of the distribution of individuals in isotopic space. The ellipses enclose the core 40% of data and so they represent the typical resource use of the analysed population (Jackson et al., 2011). The Bayesian estimate of SEA (SEA$_B$) tested differences in niche sizes between the species in the different sites and was calculated using a Markov chain Monte Carlo simulation (10^4 iterations per category) (Jackson et al., 2011, 2012). Differences in the sizes of isotopic niches (as SEA$_B$) of the species were evaluated in SIBER by calculating the probability that the relative posterior distributions of the niche sizes were significantly smaller or larger between the species ($\alpha = 0.05$). Thus, no

overlap in the 95% confidence intervals of SEA$_B$ indicated a significantly smaller/larger niche size (depending on the direction of the difference between the species). The SI data were then used to calculate isotopic niche overlap (%) between the species using SEA$_c$ in SIBER (subscript 'c' indicates a small sample size correction was used; Jackson et al., 2012). In each subsidised fishery, the extent of niche overlap between the species used carp as the comparator species as it was the largest species present.

2.3 | Experimental ponds

To test whether the experimental release of an angler subsidy results in the fish trophic niches shifting towards relatively enriched $\delta^{13}C$ values, a small pond experiment was used (Figure S1A,B; Tables S1B and S2). It was based on two cyprinid species that often feature in lacustrine fisheries in England, carp and crucian carp *Carassius carassius* ('crucian'). The ponds were located in southern England and were used between 2016 and 2019 to investigate the trophic interactions of the two species with only natural prey resources present (cf. Dominguez Almela et al., 2021). In short, three ponds (approximately 400 m^2, maximum depths of 1.2 m) were used that, prior to fish stocking in January 2016, were fishless. Equal numbers of juvenile fish had then been stocked into each pond (Figure S1B). Two ponds used each species in allopatry ($n = 100$) and one pond used the two species in sympatry ($n = 50:50$ by species) (Figure S1B). Logistical constraints had prevented the use of replicated treatments. After the conclusion of this experiment in 2019, the fish population(s) of each pond overwintered before both allopatric ponds were supplemented with an angling bait subsidy between June and September 2020. The bait used was pelletised fish meal ('pellets'; 2 mm diameter with constituents of 45% protein and 20% fish oil), as these provided a resource with distinct stable isotope data from natural prey and enabled relatively precise amounts to be released into the ponds. Correspondingly, over the 15-week treatment period in 2020, approximately 2 kg of pellets per week were released by hand into each allopatric pond, with the pellets fed into discrete areas of the ponds to replicate angling activities. In contrast, the adjacent sympatric pond did not receive any angler bait subsidy in 2020, with the trophic niche positions and sizes of the species determined according to natural prey availability and interactions between the two sympatric fish species (Figure S1B; Dominguez Almela et al., 2021).

In October 2020, the ponds were sampled using baited fish traps (21 mm fishmeal pellets), with captured fish removed, identified, measured (FL, nearest mm), anaesthetized and a fin biopsy taken. Samples of macroinvertebrates (Chironomidae and Gammaridae) were then taken as fish putative prey resources (sweep net). These samples, along with samples of the pellets that were fed as the subsidy, were dried to constant mass at 60°C and analysed at the Cornell University Stable Isotope Laboratory as previously described. As there were some differences in the macroinvertebrate SI data between the three ponds in 2020 (Table S3), and in the 2017–2019 data (Dominguez Almela et al., 2021), then the SI data were also converted to $\delta^{13}C_{corr}$ and TP.

The initial analyses used GLMMs to test differences in both $\delta^{13}C_{corr}$ and TP between the three sets of treatments for each species (allopatric no subsidy, allopatric with subsidy and sympatry, no subsidy). The dependent variable was $\delta^{13}C_{corr}$ or TP, fixed effects were treatment × species and fish length, and pond number and year were random effects. Model outputs included mean values of $\delta^{13}C_{corr}$ and TP per treatment and species combination

that were tested for the significance of their differences using pairwise comparisons (linearly independent, with Bonferroni correction for multiple comparisons). The isotopic niches (SEA_B) and the extent of isotopic niche overlap (SEA_C) were then determined for each treatment and year (as previously described). Using only data from 2020, the SEA_B and SEA_C results for the subsidised allopatric ponds were compared with the non-subsidised sympatric
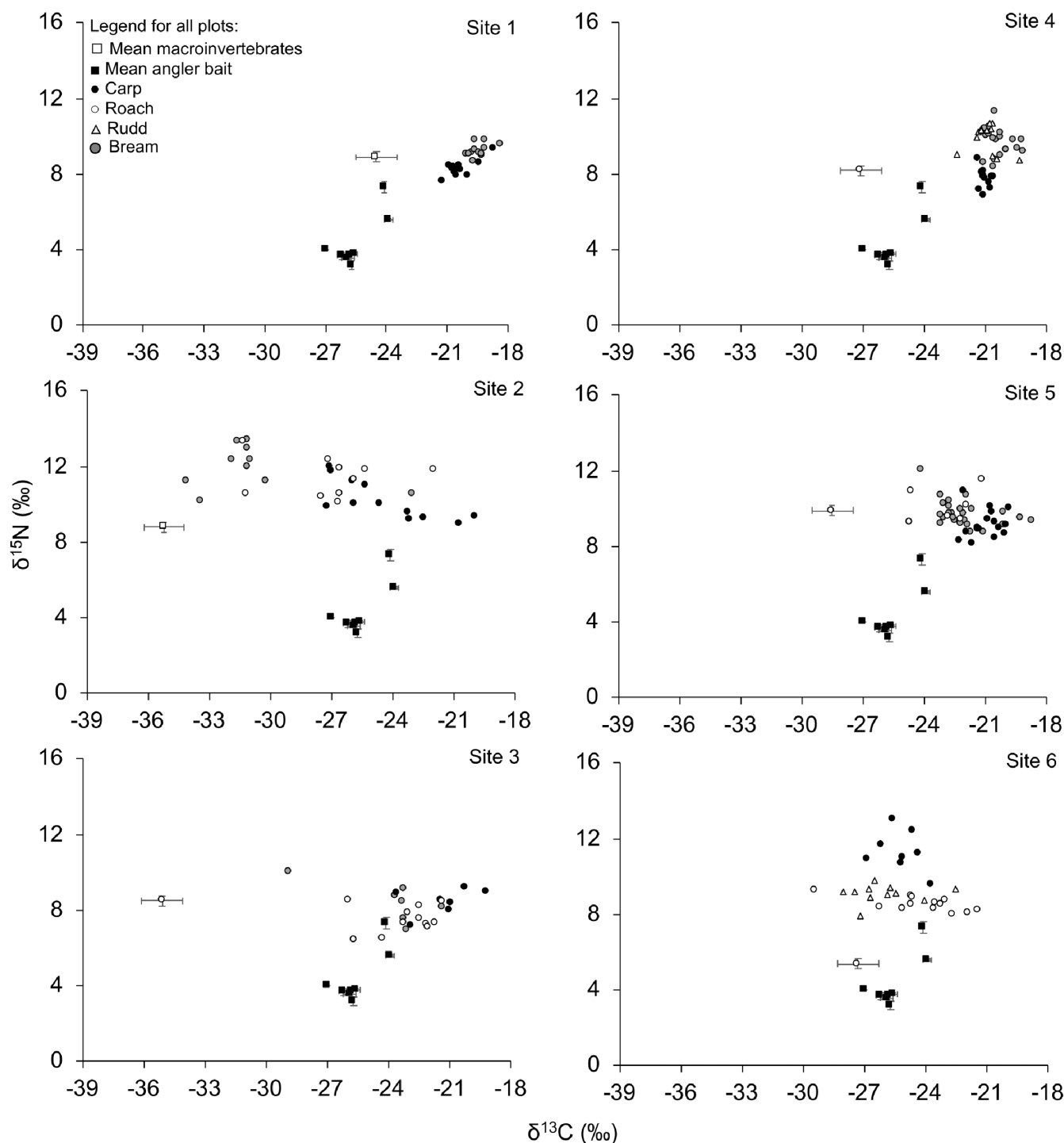

FIGURE 1 Stable isotope bi-plots of the subsidised fisheries, showing mean SI values (±95% confidence limits) for each angling bait analysed and the macroinvertebrates, and the SI data at the individual level for the analysed fish species (carp *Cyprinus carpio*, bream *Abramis brama*, roach *Rutilus rutilus* and Rudd *Scardinius erythrophalmus*).

pond to quantify differences in isotopic niche size and position (Figure S1B). Then, for each allopatric pond, the SEA$_B$ and SEA$_c$ results were compared between 2020 (subsidy presence) and 2017–2019 (subsidy absence).

The ethical approval process and all regulated procedures were completed under UK Home Office licence P47216841. All data analyses were completed in R version 4.0.5 (R Development Core Team, 2021). Where error is provided around mean values, it represents 95% confidence limits unless otherwise stated.

3 | RESULTS

3.1 | Angling baits and subsidised versus non-subsidised fisheries

The angling baits were generally $\delta^{13}C$ enriched compared with the natural macroinvertebrate putative prey resources of the subsidised fisheries and some baits were also relatively depleted in $\delta^{15}N$

(Figure 1; Tables S3 and S4). In subsidy presence, fish uncorrected stable isotope data were mostly enriched in both $\delta^{13}C$ and $\delta^{15}N$ compared with all angling baits (Figure 1; Tables S1A and S4). In contrast, the non-subsidised fisheries, the majority of the fish were depleted in $\delta^{13}C$ versus the angling baits, but strongly enriched in $\delta^{15}N$ (Figure 2).

The GLMMs for the non-subsidised fishery data revealed that for $\delta^{13}C_{corr}$, the significant fixed effects were species and fish length, but not habitat type (Table 1). For TP, species was significant, but not habitat type or fish length (Table 1). Thus, the $\delta^{13}C_{corr}$ and TP data were combined across all the non-subsidised fisheries. The GLMM testing the effects of subsidy presence/absence revealed that the subsidy significantly affected $\delta^{13}C_{corr}$ (mean subsidised vs non-subsidised $\delta^{13}C_{corr}$: 7.28 ± 2.58 vs. 0.59 ± 0.71‰; $p < 0.01$), with fish length also having a significant effect, but not species and habitat type (Table 1). The subsidy also had a significant effect on TP (mean subsidised vs non-subsidised TP: 2.14 ± 0.50 vs. 3.13 ± 0.28; $p < 0.01$), with fish species also significant in the model, but not fish length or habitat type (Table 1). In subsidy presence, the isotopic
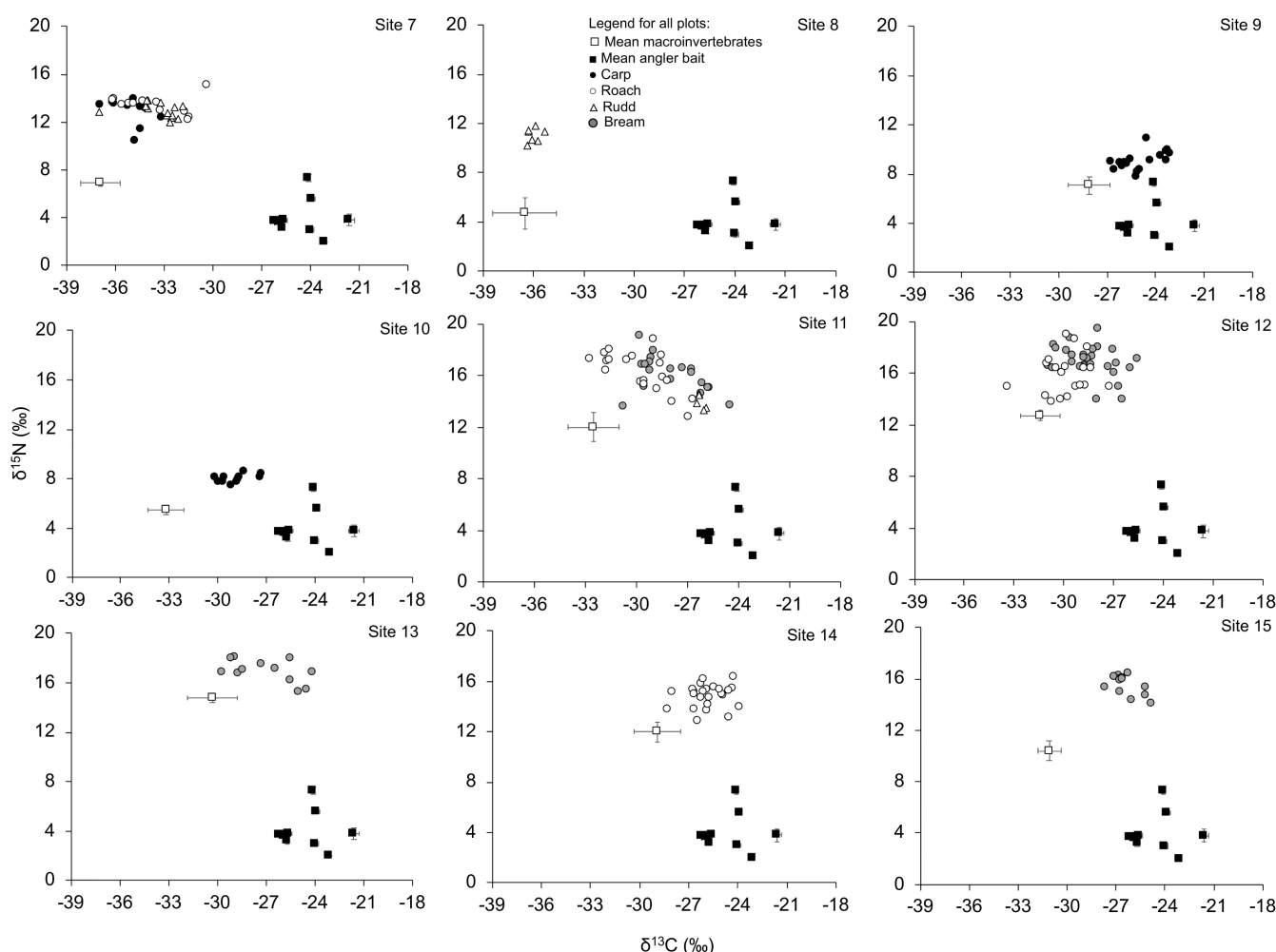
FIGURE 2 Stable isotope bi-plots of the non-subsidised fisheries, showing mean SI values (±95% confidence limits) for each angling bait analysed and the macroinvertebrates, and the SI data at the individual level for the analysed fish species (carp *Cyprinus carpio*, bream *Abramis brama*, roach *Rutilus rutilus* and Rudd *Scardinius erythrophalmus*). Note that the Y-axis differs to Figure 1 but the X-axis is standardised with Figure 1.

TABLE 1 Influence of the fixed effects of angling subsidy presence/absence, species, fish length, habitat type and experimental treatment on corrected stable isotope niche (as $\delta^{13}C_{corr}$ and trophic position, TP) of fish in the field studies and experiment from generalised linear mixed models

Test	SI metric	Fixed effect	F	p
Field: Non-subsidised fisheries	$\delta^{13}C_{corr}$	Species	$F_{3,201} = 4.38$	<0.01
		Fish length	$F_{1,201} = 7.27$	<0.01
		Habitat type	$F_{2,201} = 0.15$	0.70
	TP	Species	$F_{3,201} = 5.25$	<0.01
		Fish length	$F_{1,201} = 0.57$	0.45
		Habitat type	$F_{2,201} = 2.70$	0.10
Field: Subsidised vs non-subsidised fisheries	$\delta^{13}C_{corr}$	Subsidy presence	$F_{1,416} = 19.94$	<0.01
		Species	$F_{3,416} = 1.46$	0.23
		Fish length	$F_{1,416} = 28.20$	<0.01
		Habitat type	$F_{2,416} = 1.68$	0.20
	TP	Subsidy presence	$F_{1,416} = 11.58$	<0.01
		Species	$F_{3,416} = 7.69$	<0.01
		Fish length	$F_{1,416} = 0.41$	0.53
		Habitat type	$F_{2,416} = 0.49$	0.48
Experimental ponds	$\delta^{13}C_{corr}$	Treatment × species	$F_{5,241} = 40.66$	<0.01
		Fish length	$F_{5,241} = 3.21$	0.08
	TP	Treatment × species	$F_{5,241} = 26.78$	<0.01
		Fish length	$F_{5,241} = 1.45$	0.23

TABLE 2 Mean (±95% confidence limits) of fish fork lengths (FL) and the corrected stable isotope values ($\delta^{13}C_{corr}$ and TP) for each fish species for the non-subsidised and subsidised wild populations (combined data for all sites)

Species	Treatment	n	FL (mm)	$\delta^{13}C_{corr}$ (‰)	TP
Bream	Non-subsidised	75	298 ± 32 (266, 331)	1.5 ± 0.2 (1.3, 1.7)	3.1 ± 0.1 (3.0, 3.2)
	Subsidised	75	282 ± 21 (261, 303)	7.4 ± 0.6 (6.9, 8.0)	2.2 ± 0.1 (2.1, 2.3)
Carp	Non-subsidised	38	97 ± 14 (83, 111)	1.3 ± 0.2 (1.1, 1.5)	2.9 ± 0.2 (2.7, 3.1)
	Subsidised	82	441 ± 36 (404, 477)	8.0 ± 0.6 (7.3, 8.6)	2.2 ± 0.1 (2.1, 2.3)
Roach	Non-subsidised	73	149 ± 16 (133, 166)	0.8 ± 0.1 (0.7, 1.0)	3.2 ± 0.1 (3.1, 3.3)
	Subsidised	41	153 ± 10 (142, 163)	5.7 ± 1.1 (4.5, 6.9)	2.5 ± 0.2 (2.3, 2.6)
Rudd	Non-subsidised	26	107 ± 19 (89, 126)	1.1 ± 0.3 (0.8, 1.4)	3.6 ± 0.2 (3.4, 3.8)
	Subsidised	23	120 ± 17 (102, 139)	4.3 ± 1.5 (2.7, 5.8)	2.8 ± 0.1 (2.6, 2.9)

niches of all fish species were substantially larger, enriched in $\delta^{13}C_{corr}$ and of lower TP versus subsidy absence (Table 2; Figure 3). Only rudd had isotopic niches that had some overlap between the non-subsidised and subsidised fisheries (Table 3; Figure 3). There were interspecific differences in both $\delta^{13}C_{corr}$ and TP in most sites (Table 4), with these reflected in the niche overlaps between species being low and never exceeding 39% (Table 5; Figure 4).

3.2 | Experimental ponds

The pelletised fishmeal used as the angling subsidy in 2020 was substantially enriched in $\delta^{13}C$ compared to the putative macroinvertebrate prey resources, although differences in $\delta^{15}N$ were relatively minor (Tables S3 and S4). The GLMMs revealed that both $\delta^{13}C_{corr}$ and TP were significantly influenced by treatment × species, but

not fish length (Table 1). The effect of the subsidy on the allopatric carp and crucians was to significantly enrich their $\delta^{13}C_{cor}$ values compared to all other treatment combinations ($p < 0.01$ in all cases), whereas TP was shifted to an intermediate position between the allopatric (no subsidy) and sympatric treatments (Figure S2).

In 2020, carp stable isotope niche sizes (as SEA_b) were significantly larger in subsidy presence than in absence (Table 6a; Figure 5a), driven by the enriched $\delta^{13}C_{corr}$ of some individuals (Table 6a). There was only minor overlap of these niches (Table 6a). Allopatric carp isotopic niches were relatively small in subsidy absence (2017–2019), but were substantially larger in subsidy presence in 2020, with only minor niche overlap between these periods (3%–11%; Table 6b; Figure 5b). For crucians, there was no isotopic niche overlap in subsidy presence and absence in 2020, with the subsidised niche being highly $\delta^{13}C_{corr}$ enriched (Figure 5c), but with the niches not differing significantly in size (Table 6a; Figure 5c). Allopatric crucian stable

isotope niches were larger in subsidy presence (2020) versus subsidy absence (2017–2019), with no overlap between the two periods (Table 6b; Figure 5d).

4 | DISCUSSION

The results indicated that in freshwaters where angling activity is high, inputs of baits by anglers (groundbaits, seeds, boilies and/or pellets) can provide a strong trophic subsidy for fish, resulting in substantial δ^{13}C enrichment in their isotopic positions and niches, as predicted. This δ^{13}C enrichment was, however, much less evident in the analysed macroinvertebrates, with their samples generally being δ^{13}C depleted versus bait. Despite the substantial δ^{13}C enrichment of the fish isotopic niches in the subsidised fisheries, patterns of interspecific niche divergence were still evident at the site level, contrary to prediction. The experimental release of an angler subsidy resulted in fish isotopic niches shifting towards relatively enriched δ^{13}C values, resulting in the isotopic positions and niches being distinct for both species in allopatry between subsidy presence and absence, with these niches also being distinct from when the species were in sympatry in subsidy absence.

It was apparent that, when compared to the non-subsidised fisheries, the four analysed fish species in the subsidised fisheries all demonstrated isotopic niche shifts away from macroinvertebrate prey resources and towards the enriched δ^{13}C of the angling subsidies. This is consistent with other studies on angling subsidies. For example, Mehner et al. (2019) revealed that after a 3-month exposure period to these baits in a German lake, some omnivorous cyprinid species had diets comprising substantial amounts of these baits. Adult European barbel in 11 English rivers all showed patterns of strong δ^{13}C enrichment away from macroinvertebrate putative prey resources, with this enrichment associated with the high consumption of marine fishmeal baits (De Santis et al., 2019), with this also apparent in adult chub *Squalius cephalus* (Gutmann Roberts & Britton, 2018).

It was also apparent that the four fish species in the subsidised fisheries still had relatively distinct isotopic niches, despite their general consumption of angler subsidies. There are a number of potential reasons why this niche divergence remained apparent in subsidy presence. Although the baits analysed for their stable isotope data all showed δ^{13}C enrichment and, generally, δ^{15}N depletion, there was still considerable isotopic variation between them, thus species-specific consumption of certain baits could have driven niche divergence. This divergence would also be influenced by the different bait sizes, with the smallest particles being in groundbait and the largest baits being boilies and pellets (Imbert et al., 2022). These baits are recognised as being size-selective in angling, with bigger baits only capable of ingestion by fish with a sufficiently large gape (Sánchez-Hernández et al., 2019). Thus, the niche divergence between carp
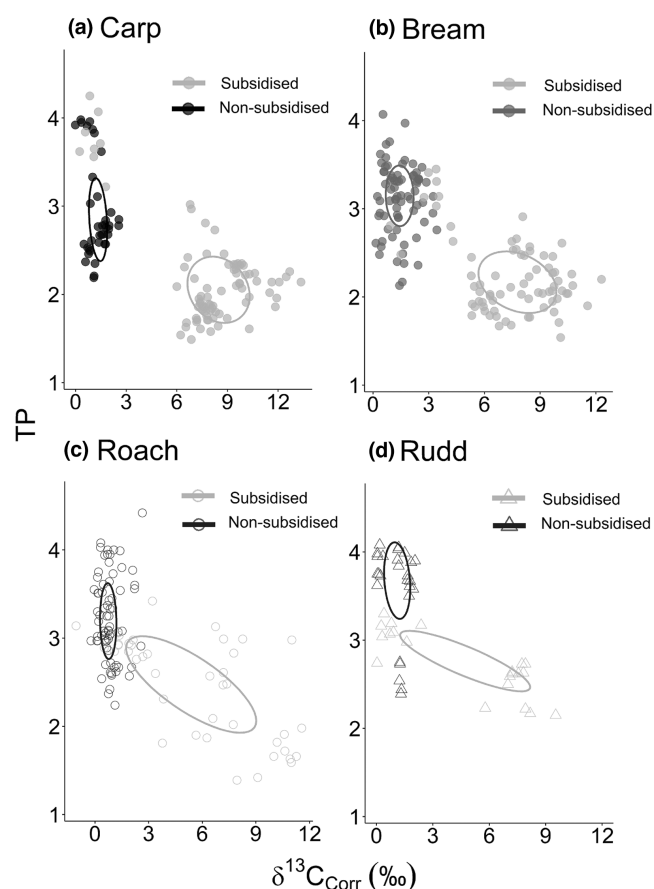

FIGURE 3 Isotopic niches (as standard ellipse areas, SEAc) for the analysed fish species in non-subsidised versus subsidised fisheries (carp *Cyprinus carpio*, bream *Abramis brama*, roach *Rutilus rutilus* and Rudd *Scardinius erythrophalmus*). TP, trophic position (calculated from δ^{15}N data); δ^{13}C$_{corr}$, corrected value of δ^{13}C.

TABLE 3 Isotopic niche sizes (as standard ellipse areas, SEAc and SEAb, with 95% CI) and ellipses overlap for each species and treatment (non-subsidised and subsidised)

Species	Treatment	SEA$_c$ (CI)	SEA$_b$ (CI)	Overlap
Carp	Non-subsidised	1.00 (0.37, 1.74)	0.95 (0.70, 1.34)	0%
	Subsidised	4.12 (−0.41, 12.20)	4.02 (3.27, 5.11)	
Bream	Non-subsidised	1.02 (−0.16, 2.42)	1.00 (0.79, 1.25)	0%
	Subsidised	2.94 (−0.78, 9.04)	2.84 (2.31, 3.65)	
Roach	Non-subsidised	0.92 (−0.38, 2.45)	0.89 (0.71, 1.12)	0%
	Subsidised	5.07 (0.32, 13.85)	5.01 (3.59, 6.78)	
Rudd	Non-subsidised	1.17 (0.85, 1.50)	1.08 (0.75, 1.65)	6%
	Subsidised	2.31 (1.07, 3.68)	2.30 (1.54, 3.64)	

TABLE 4 Mean (95% CI) of fish fork lengths and the corrected stable isotope values ($\delta^{13}C_{corr}$ and TP; 95% CI) for each species for the subsidised fisheries

Site	Species	n	FL (mm)	$\delta^{13}C_{corr}$ (‰)	TP
1	Bream	12	387 (345, 430)	10.1 (9.5, 10.7)	2.1 (2.0, 2.2)
	Carp	12	570 (534, 605)	8.3 (7.4, 9.2)	1.8 (1.7, 1.9)
2	Bream	10	168 (128, 208)	3.6 (1.8, 5.4)	3.0 (2.8, 3.3)
	Carp	12	373 (342, 403)	9.0 (7.7, 10.3)	2.5 (2.3, 2.7)
	Roach	10	145 (128, 162)	6.8 (5.2, 8.5)	2.9 (2.6, 3.1)
3	Bream	7	236 (165, 308)	9.5 (7.7, 11.3)	2.0 (1.7, 2.3)
	Carp	7	473 (402, 545)	11.6 (10.8, 13.0)	2.0 (1.7, 2.2)
	Roach	11	167 (148, 187)	10.1 (9.2, 10.9)	1.7 (1.6, 1.8)
4	Bream	18	308 (266, 350)	8.4 (8.0, 8.7)	2.4 (2.3, 2.5)
	Carp	12	499 (432, 565)	7.5 (7.3, 7.7)	1.9 (1.8, 2.0)
	Rudd	12	141 (115, 167)	7.6 (7.0, 8.1)	2.5 (2.3, 2.6)
5	Bream	28	272 (249, 294)	6.6 (6.1, 7.1)	1.9 (1.9, 2.0)
	Carp	15	564 (508, 619)	7.6 (7.1, 8.0)	1.8 (1.7, 1.9)
	Roach	6	128 (95, 161)	5.6 (4.0, 7.1)	2.1 (1.8, 2.4)
6	Carp	8	525 (482, 568)	1.0 (0.6, 1.5)	3.7 (3.5, 4.0)
	Roach	14	158 (135, 181)	1.5 (1.0, 2.1)	3.0 (2.9, 3.0)
	Rudd	11	98 (76, 121)	0.6 (0.1, 1.6)	3.1 (3.0, 3.2)

TABLE 5 Isotopic niche sizes (standard ellipse areas, SEAc and SEAb, with 95% CI) per species and fishery site

Site	Species	SEA$_c$ (CI)	SEA$_b$ (CI)	Overlap with carp (%)
1	Carp	0.36 (0.19, 0.55)	0.35 (0.19, 0.64)	—
	Bream	0.28 (0.15, 0.39)	0.24 (0.14, 0.45)	0%
2	Carp	1.34 (0.89, 1.81)	1.22 (0.73, 2.41)	—
	Bream	2.88 (1.88, 4.28)	2.32 (1.28, 4.74)	0%
	Roach	2.37 (1.40, 3.46)	1.85 (1.02, 4.01)	39%
3	Carp	0.87 (0.68, 1.09)	0.68 (0.28, 1.59)	—
	Bream	1.60 (1.27, 1.96)	1.37 (0.48, 3.23)	26%
	Roach	0.92 (0.52, 1.32)	0.78 (0.42, 1.48)	14%
4	Carp	0.14 (0.09, 0.19)	0.12 (0.07, 0.24)	—
	Bream	0.54 (0.24, 0.85)	0.49 (0.30, 0.80)	0%
	Rudd	0.67 (0.44, 0.97)	0.58 (0.47, 0.71)	0%
5	Carp	0.58 (0.25, 0.96)	0.50 (0.32, 0.89)	—
	Bream	0.74 (0.21, 1.29)	0.70 (0.48, 1.02)	23%
	Roach	1.48 (1.20, 1.70)	1.06 (0.45, 2.81)	0%
6	Carp	0.55 (0.39, 0.77)	0.43 (0.21, 0.96)	—
	Roach	0.26 (0.13, 0.39)	0.23 (0.14, 0.43)	0%
	Rudd	0.39 (0.20, 0.60)	0.33 (0.18, 0.64)	0%

and rudd could have been driven by their considerable differences in body and gape size, where carp have a large gape (Rapp et al., 2008). However, rudd also tend to consume natural prey of pelagic origin (Guinan Jr et al., 2015), whereas carp are more benthivorous (Vilizzi et al., 2015). Correspondingly, rudd in the subsidised fisheries might also have been maintaining some exploitation of natural pelagic resources (as also suggested by their sharing of isotopic niche space with rudd in the non-subsidised fisheries). Conversely, bream and carp are trophically analogous, with their foraging involving sucking sediment into the buccal cavity, selecting food by filtering it with the gills, and then expelling the remainder into the water column (Hansen et al., 2019; Sibbing, 1988). Nevertheless, their isotopic niches only overlapped in two subsidised sites, with no overlap in three others, with this divergence also potentially driven by the considerable differences between the species in their body/gape sizes (carp being larger in samples) (Sánchez-Hernández et al., 2019).
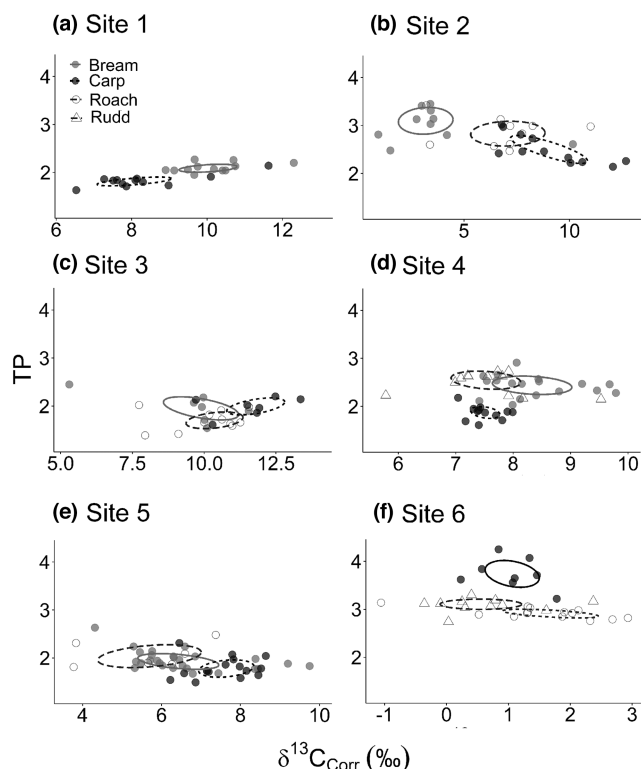
FIGURE 4 Isotopic niches (as standard ellipse areas, SEAc) of the analysed fishes in the subsidised fisheries (sites 1–6; carp *Cyprinus carpio*, bream *Abramis brama*, roach *Rutilus rutilus* and Rudd *Scardinius erythrophalmus*). TP, trophic position (calculated from $\delta^{15}N$ data); $\delta^{13}C_{corr}$, corrected value of $\delta^{13}C$. Note the differences in the values on the *X*-axis that enable the extent of interspecific differences in niche sizes to be better observed.

Although the angling subsidies provided fish with a novel food resource, the SI data from the analysed macroinvertebrates suggested there were minimal effects on their stable isotope values as these remained relatively depleted in $\delta^{13}C$ versus the angling baits. Although the macroinvertebrate sampling was only designed to provide samples of putative fish prey for SIA, the results were consistent with those of Mehner et al. (2019) who also found minor effects on non-fish taxa over a 3-month bait exposure period. In rivers where European barbel diet comprises of large proportions of marine fishmeal baits, there is also no evidence that this fishmeal is being also used by Gammarus spp. (De Santis et al., 2019; Gutmann Roberts et al., 2017). Conversely, in aquaculture, similar novel trophic subsidies have strongly influenced non-fish taxa where, for example, approximately 65% of *Daphnia* spp. body carbon was ultimately derived from pelletised fishmeal originating from an in-situ fish farm on Esthwaite Water, England (Grey et al., 2004). Although these wider trophic effects were not apparent here, this might be due to the amounts of formulated feed being released into the environment being substantially higher during aquaculture activities.

The experimental ponds provided the opportunity for testing the response of the fish isotopic ecology to the controlled release of an angling subsidy. While the lack of treatment replication limits some of the inferences on the generality of the patterns and processes detected, the two allopatric treatments and the sympatric treatment had strong temporal replication by running between 2016 and 2019 in subsidy absence. In this period, the isotopic niches of both fish species were strongly associated with the putative macroinvertebrate prey, with differences in the fish isotopic niches between allopatry and sympatry resulting from processes including intraspecific

TABLE 6 (a) Isotopic niche sizes (standard ellipse areas, SEAc and SEAb, with 95% CI) and ellipse overlap per species and treatment. (b) Isotopic niche sizes (standard ellipse areas, SEAc and SEAb, with 95% CI) and ellipses overlap between 2017 and 2019 (angling subsidy absence) and 2020 (angling subsidy presence) by species in each allopatric pond

| (a)				
Species	**Treatment**	**SEA$_c$ (CI)**	**SEA$_b$ (CI)**	**Overlap**
Carp	Non-subsidised	0.32 (0.11, 0.55)	0.30 (0.18, 0.47)	18%
	Subsidised	0.85 (0.41, 1.28)	0.83 (0.51, 1.38)	
Crucian	Non-subsidised	0.22 (0.08, 0.36)	0.19 (0.12, 0.33)	0%
	Subsidised	0.55 (0.29, 0.85)	0.50 (0.31, 0.82)	
(b)				
Species	**Year**	**SEA$_c$ (CI)**	**SEA$_b$ (CI)**	**Overlap with 2020**
Carp	2017	0.18 (0.10, 0.28)	0.17 (0.10, 0.28)	11%
	2018	0.13 (0.09, 0.17)	0.11 (0.07, 0.20)	2%
	2019	0.10 (0.07, 0.12)	0.08 (0.05, 0.16)	3%
	2020	0.85 (0.41, 1.28)	0.83 (0.51, 1.38)	—
Crucian	2017	0.14 (0.07, 0.20)	0.12 (0.07, 0.23)	0%
	2018	0.15 (0.10, 0.19)	0.13 (0.07, 0.25)	0%
	2019	0.08 (0.04, 0.11)	0.07 (0.06, 0.08)	0%
	2020	0.55 (0.29, 0.85)	0.50 (0.31, 0.82)	—
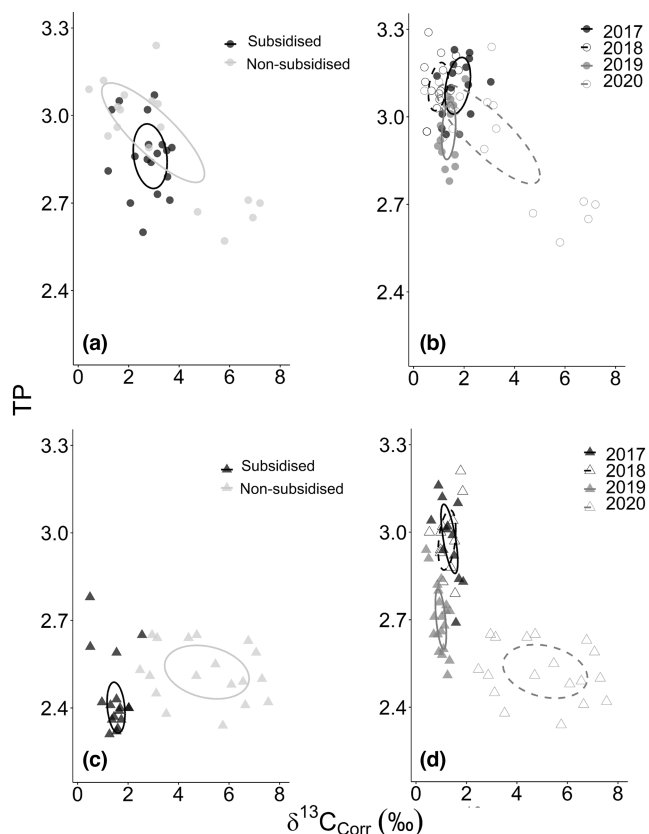
FIGURE 5 Isotopic niches (as standard ellipse areas, SEAc) of carp *Cyprinius Carpio* and crucian carp *Carassius carassius* in the experimental ponds, where comparisons are between (a) carp in the subsidised versus non-subsidised ponds in 2020; (b) carp in the subsidised ponds in 2017, 2018, 2019 and 2020; (c) crucian carp in the subsidised versus non-subsidised ponds in 2020; and (d) crucian carp in the subsidised ponds between 2017, 2018, 2019, and 2020. TP, trophic position (calculated from $\delta^{15}N$ data); $\delta^{13}C_{corr}$, corrected value of $\delta^{13}C$.

and interspecific competition (Dominguez Almela et al., 2021). The addition of the subsidy to the allopatric treatments in 2020 then resulted in substantial isotopic niche shifts towards enriched $\delta^{13}C$ values in both fishes, with the isotopic niches in the non-subsidised sympatric treatment remaining relatively similar to previous years. This substantial effect of the subsidy on the fish isotopic niches was thus consistent with the patterns detected in the subsidised fisheries, as well as in other studies (e.g. Bašić & Britton, 2016; Mehner et al., 2019). Within the experiment, testing whether the addition of the subsidy could disrupt the isotopic patterns between the fish species in sympatry was not feasible, so this also remains an outstanding requirement for further work. In addition, further studies on angling subsidies more generally should also consider generating quantitative estimates on the bait inputs being released into the waterbodies being used for angling to enable more accurate testing of their trophic effects. Here, qualitative categories of 'high' versus 'low' angling activities and bait inputs were used and, while there was confidence that these provided a robust categorisation of bait inputs and rigorous testing of their trophic effects, it is also likely

that a gradient of subsidy inputs exists across angled lowland freshwaters more generally that involves the release of a wide range of different baits.

The use of angler baits can strongly influence the trophic ecology of individual species within riverine fisheries (De Santis et al., 2019; Nolan et al., 2019). The short-term release of these baits has also resulted in their important contribution to the diets of omnivorous cyprinid fishes (Mehner et al., 2019). Here, we demonstrate for the first time that their trophic effects are ubiquitous, substantially enriching isotopic niches in $\delta^{13}C$ in all fishes and fisheries where they are used in relatively high quantities through their direct consumption, but not resulting in isotopic niche convergence. Correspondingly, the release and subsequent consumption of these baits can artificially elevate the carrying capacity of freshwater ecosystems, potentially leading to increased fish production and individual fish mass (Mehner et al., 2019). Thus, the managed release of these baits by managers into recreational fisheries should benefit catch rates and increase angler satisfaction (Arlinghaus & Niesar, 2005). Fish stocking into inland waters for angling enhancement is also commonplace in industrialised countries, with the release of an additional 1.5 kg of fish biomass per angler per year (Cucherousset et al., 2021). Consequently, the regular release of these baits by fishery managers and/or anglers into stocked fisheries should provide additional food resources to support this elevated biomass, which should minimise their top-down effects on natural prey communities and potentially reduce competitive interactions between the resident and stocked fishes, although this remains to be quantified empirically.

The use of these baits to reduce the strength of top-down effects of the fish on their natural prey resources can also be used in ecological enhancement schemes in ecosystems with high anthropogenic pressures. For example, carp and common bream can both impact the ecological functioning of lakes through middle out effects involving processes that are top-down (depleting macroinvertebrate and zooplankton communities) and bottom-up (increasing turbidity and reducing macrophyte biomass) (Vilizzi et al., 2015; Weber & Brown, 2009). These effects are often managed in lake restoration by biomanipulation programmes that reduce—or even eliminate—cyprinid fish biomass (Dalu et al., 2020; Triest et al., 2016). Thus, managed inputs of these baits could substantially reduce the top-down effects of cyprinid fishes on natural prey communities through provision of alternative food resources. However, the bottom-up effects of these fishes are likely to be unaffected, plus there is the issue of these baits often being nutrient rich, so potentially exacerbating eutrophication issues if used excessively (Amaral et al., 2013). Consequently, managers must be aware that while the application of these baits within fishery activities and ecological enhancement schemes can be positive, there is also a risk that their use can contribute to ecological degradation, such as exacerbating eutrophication (Arlinghaus & Mehner, 2003) and the introduction of pollutants that include microplastics (de Carvalho et al., 2021).

The results presented here on the extent to which fish in recreational fisheries consume these baits also raise issues around

angling ethics, given their use is likely to increase fish capture rates (Cooke et al., 2021). In catch-and-release fisheries, this also raises welfare considerations through the potential for individual fish to be captured repeatedly (Britton et al., 2007; Browman et al., 2019). In entirely, while we suggest that these baits can provide substantial benefits to both fish and fisheries via their direct consumption when used in appropriated quantities and quality, we also emphasise that managers must thus also consider the effects of these baits on fish welfare, angling ethics, and ecosystem integrity and functioning.

AUTHORS' CONTRIBUTIONS

J.R.B. and J.C. designed the concept and study design; V.D.A. led the analyses; J.R.B. and V.D.A. led writing, assisted by J.C. All authors contributed to revising the manuscript and approved its submission.

CONFLICT OF INTEREST

The authors declare no conflicts of interest. J. Robert Britton is an Associate Editor of Journal of Applied Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.k98sf7m86 (Britton et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.