

Consistent patterns in trophic partitioning between sympatric salmonid fishes in two rivers of contrasting productivity

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Abstract – In environments with limited prey resources, coexisting and morphologically similar species that share these resources can compete strongly, potentially resulting in competition and trophic niche displacement. Alternatively, they can partition in their resource use to minimise their competitive interactions. Here, the trophic relationships of two sympatric salmonid fishes, brown trout *Salmo trutta* and Atlantic salmon *Salmo salar*, were assessed in two contrasting rivers, a chalk stream where the fish were very fast growing, and an upland stream where the fish were relatively slow growing. Using stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), the size and position of their stable isotope niches were assessed when the species were sympatric and, in the upland stream, compared between allopatry and sympatry. In both rivers and all sympatric sites, strong patterns of inter-specific stable isotope niche partitioning were evident. In both species in the upland stream, there were only minor differences between their isotope data between allopatry and sympatry, with the position of their isotopic niche similar in both contexts and with overlap in the 95% credible intervals of their isotopic niche sizes. This suggests inter-specific differences in their trophic ecology were driven by differences in functional morphology and habitat use than inter-specific interactions.

Keywords: Stable isotope analysis / chalk stream / Atlantic salmon / brown trout

1 Introduction

The trophic dynamics and competitive interactions of populations within communities are important in determining food web structure (Woodward and Hildrew, 2002; George and Collins, 2024) and has potentially important implications for individuals within migratory populations (Lizé *et al.*, 2023). In environments where prey resources are limiting, the coexistence of closely related and morphologically similar species that share these resources compete intensely and where their competitive interactions are asymmetric, this can potentially result in competitive displacement (Cucherousset *et al.*, 2012; Kakareko *et al.*, 2013). Alternatively, these sympatric competitive interactions in resource limited systems can lead to niche partitioning, where the species exploit different food resources (MacArthur, 1965; Ross *et al.*, 1985). However, trophic niche overlaps can remain between species where resources are unlimited and / or the species have insufficient

adaptive capacity to switch to alternative prey (Abrams *et al.*, 2006; Bauduin *et al.*, 2013; Cucherousset *et al.*, 2020). In allopatry, the absence of inter-specific competition can result in the species exploiting a wider range of resources than in sympatry, with reduced dietary specialisms (Tran *et al.*, 2015). Where niches remain similar between sympatric and allopatric contexts, this can be due to functional constraints in the species, where the niche conservation hypothesis suggests species will retain their niche through space and time, irrespective of context (Comte *et al.*, 2017).

Somatic growth rates and body sizes at age of fish are associated with prey resource quality and quantity, so inter-population differences in these metrics can reflect differences in the productivity of the ecosystems (Tanner *et al.*, 2019; Lai *et al.*, 2024). These differences in productivity could then be important in influencing how life history strategies are expressed within the coexisting species, especially if these are anadromous (Simmons *et al.*, 2022). Atlantic salmon *Salmo salar* populations generally express obligate anadromy, where the majority of their growth and development occurs in marine environment, whereas brown trout *Salmo trutta* tend

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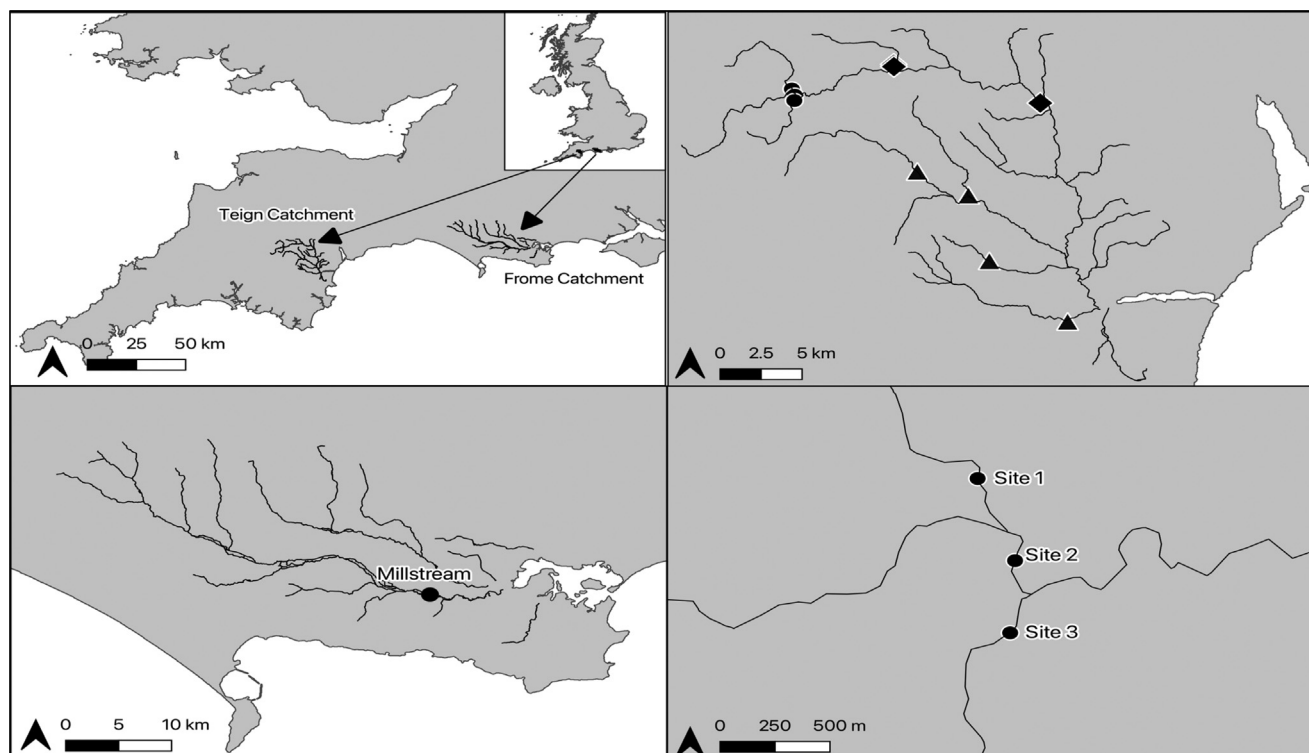


Fig. 1. Main: locations of the River Teign and River Frome in Southern England; bottom left: location of the Millstream study site on the River Frome; top right: sampling areas on the River Teign with sympatric populations (circles), allopatric salmon (diamonds) and allopatric trout (triangles) (*cf.* Tabs. 1 and 3); bottom right: core sympatric Teign sites.

to express facultative anadromy, where within populations, some individuals express anadromy and others remain as river residents (Jonsson and Jonsson, 2021). These salmonid species coexist across much of their respective ranges, including across a wide range of river types, from nutrient rich chalk streams to nutrient poor upland streams (Crisp, 1993; Simmons *et al.*, 2021). As they also have relatively similar functional morphologies and ecological requirements (Johnson and Johnson, 2011), sympatric populations have the potential to consume similar prey resources. However, communities of sympatric salmonid populations often express strong patterns of inter-specific ecological and trophic niche partitioning (Eloranta *et al.*, 2013). This partitioning often becomes strongly apparent during ontogenetic development, when individuals within populations become increasingly specialised in their resource use (Jørgensen *et al.*, 2000; Sánchez-Hernández and Cobo, 2016). Lake dwelling populations of Atlantic salmon and brown trout are often generalist foragers with a broad diet, but with individuals increasingly specialising on lower numbers of prey items as they grow, with inter-specific niche divergence becoming increasingly evident (Jørgensen *et al.*, 2000). The opportunity for populations of the two species to compete for prey resources is elevated in streams where their spatial niche overlaps can be considerable, although juvenile salmon tend to be in faster flowing and shallower habitats than brown trout, with salmon habitat use also restricted by interactive segregation due to aggressive interspecific competitive interactions from the trout (Heggenes *et al.*, 1999).

The aim of this study was to assess the interspecific trophic interactions between Atlantic salmon (“salmon”) and brown trout (“trout”) in two streams in Southern England that differed markedly in the somatic growth rates of both species using stable isotope analysis (SIA). The analyses of their growth rates and stable isotope ecology enabled testing of whether the sympatric populations expressed trophic (stable isotope) niche partitioning or overlap in both streams, and whether these patterns were influenced by their growth rates. In addition, samples were also collected from one of the streams from areas where either salmon or trout were in allopatry, enabling testing of the niche conservation hypothesis through comparison for each species of their stable isotope niche sizes and positions between sympatry and allopatry.

2 Materials and methods

2.1 Study areas and fish sampling

The two rivers were the River Frome and the River Teign in Southern England (Fig. 1). The Frome is a lowland chalk-stream in that flows for approximately 70 km from its source (50.50. 24°N; 02.36. 12°W) to its tidal limit (50.40. 38°N; 02.07. 30°W). There is a fish assemblage of approximately 15 species present, with non-salmonid species comprising of several species of cypriniforms that are numerically dominated by European minnow *Phoxinus Phoxinus*. However, the river is most recognised for its regionally significant populations of salmon and trout (Simmons *et al.*, 2020; Marsh *et al.*, 2020). The site sampled was on a millstream of approximately 2 km

Table 1. Location (as latitude/ longitude), sample dates and sizes by river, site and species for Atlantic salmon *Salmo salar* (“salmon”) and brown trout *Salmo trutta* (“trout”), their mean fork length (“length”), mean stable isotope data (as $\delta^{13}\text{C}$ or $\delta^{13}\text{C}_{\text{corr}}$ (Eq. (2)) and $\delta^{15}\text{N}$ or trophic position (TP; Eq. (1), and their stable isotope niche metrics, where TA: the total area of the convex hull encompassing the data points, SEA: the Standard Ellipse Area containing 40% of the data, SEA_C : Correction applied to SEA to account for small sample sizes, and the Bayesian estimate for SEA (SEA_B), expressed by their 95% credible intervals. All values in parentheses are standard deviation.

River/ site/ location	Sample date	Species	N	Length (mm)	$\delta^{13}\text{C}/\delta^{13}\text{C}_{\text{corr}}$ (‰)	$\delta^{15}\text{N}/\text{TP}$	TA	SEA	SEA_C	SEA_B (95%CI)
Frome 50.67952, –2.18163	July 2008	Salmon	36	75 (8)	–30.31 (0.74)	11.72 (0.41)	2.77	0.76	0.79	0.5–1.1
		Trout	27	128 (72)	–28.78 (0.89)	13.20 (1.03)	6.67	2.1	2.18	1.4 – 3.1
	Sept 2008	Salmon	55	90 (10)	–30.56 (0.63)	13.64 (0.73)	5.16	1.41	1.43	1.1 – 1.8
		Trout	42	134 (44)	–29.06 (0.89)	14.29 (0.77)	9.09	2.09	2.15	1.5 – 2.8
Teign, Site 1 50.67997, –3.86823	Sept 2022	Salmon	17	101 (20)	–0.27 (0.5)	3.89 (0.2)	0.67	0.26	0.28	0.2 – 0.4
		Trout	21	145 (57)	1 (0.6)	3.4 (0.2)	0.82	0.3	0.32	0.2 – 0.5
	July 2023	Salmon	14	100 (23)	–0.38 (0.6)	3.61 (0.2)	0.61	0.27	0.29	0.2 – 0.5
		Trout	15	140 (60)	1.2 (0.4)	3.38 (0.2)	0.75	0.32	0.34	0.2 – 0.5
Teign, Site 2 50.67724, –3.87072	Sept 2022	Salmon	14	99 (26)	1.48 (0.5)	3.38 (0.2)	0.51	0.26	0.28	0.1 – 0.4
		Trout	12	157 (48)	2.1 (0.5)	2.97 (0.3)	0.67	0.31	0.34	0.2 – 0.6
	July 2023	Salmon	15	96 (27)	1.21 (0.6)	3.15 (0.2)	1.06	0.43	0.46	0.2 – 0.7
		Trout	14	161 (69)	2.31 (0.7)	3.16 (0.3)	1.73	0.66	0.72	0.4 – 1.1
Teign, Site 3 50.67376, –3.86968	Sept 2022	Salmon	14	103 (25)	1.02 (0.6)	3.94 (0.2)	0.73	0.29	0.31	0.2 – 0.5
		Trout	19	109 (37)	1.1 (0.4)	3.61 (0.2)	0.55	0.21	0.23	0.1 – 0.3
	July 2023	Salmon	15	104 (16)	0.91 (0.9)	3.79 (0.2)	1.50	0.62	0.67	0.3 – 1.0
		Trout	16	128 (39)	1.34 (0.6)	3.63 (0.2)	0.71	0.28	0.30	0.2 – 0.5

length with connections at the upstream and downstream end to the main river (Fig. 1), with the stream comprising of a series of pool/ riffle habitats where depths rarely exceeded 1 m and channel widths were to 6 m (Fig. 1). The fish assemblage was sampled using generator powered electric fishing, with samples collected in July 2008 and September 2008 (Cucherousset *et al.*, 2011). The River Teign is an upland spate river in Devon, southern England (Fig. 1), which flows approximately 50 km from its source (50°38'19.0" N; 3°57'31.0" W) to its tidal limit below Newton Abbot (50°32'10.8"; N 3°35'13.7" W). Its fish assemblage is largely dominated by brown trout (anadromous and non-anadromous forms) and salmon (all assumed anadromous), but has low diversity and abundances of other fishes, with minnow *Phoxinus phoxinus*, bullhead *Cottus gobio* and stone loach *Barbatula barbatula* mainly being present. Three focal reaches were used for repeated sampling that were located in the upper catchment: Blackaton Brook (Site 1), the North Teign (Site 2) and South Teign (Site 3) (Fig. 1). These sites were selected for the consistency in their relatively high populations of juvenile salmonids in historical surveys (WRT 2022). All the sites comprised of a series of pool and riffle sequences, with the major differences being in their physical characteristics. Site 1 was a relatively small tributary of maximum width 5 m and depths to 0.8 m, Site 2 was up to 10 m wide with depths to 1.3 m, whereas Site 3 was more regulated in its flows due to the influence of a water supply reservoir upstream (Fernworthy Reservoir), and was of maximum width 6 m with depths to 1 m. These sites were sampled using back-pack electric fishing (SmithRoot, LR24) in September 2022, July 2023 and September 2023. Although in relatively close

proximity, mark-recapture events using passive integrated transponder (PIT) tags revealed negligible mixing of fish between the sites across the sampling periods, so each site was considered independent. In addition, a further 7 sites across the River Teign catchment were sampled in late August 2023 using back-pack electric fishing, where 3 comprised of samples of allopatric salmon and 4 of allopatric trout (Fig. 1).

In all surveys on both rivers, following their capture, the fish were anaesthetised (M222), identified to species and measured (fork length, nearest mm). A sample of scales was taken from below the dorsal fin but above the lateral line and stored in a paper envelope for subsequent age analyses. A pelvic fin clip was taken for SIA. All fish were then held in clean river water for recovery to normal behaviour and were then returned to the area of river where they were captured. Fish sample sizes are provided in Table 1. Concomitantly, putative macro-invertebrate fish prey resources were then collected from sites using a sweep net (250 mm wide; 0.3 m bag depth; 250 μm mesh).

2.2 Growth rate analyses

To assess differences in trout growth rates between the rivers, scales were viewed under a projecting microscope (x48 magnification), an age estimate was derived for each individual, and their lengths at the last annulus determined ('length at age' hereafter). The length-at-age trout data for all both rivers were then combined into a single dataset and a linear regression model fitted where age was the independent variable and length at the last annulus was the dependent variable. The standardised residuals of length at the last annulus of each individual trout were then determined from the

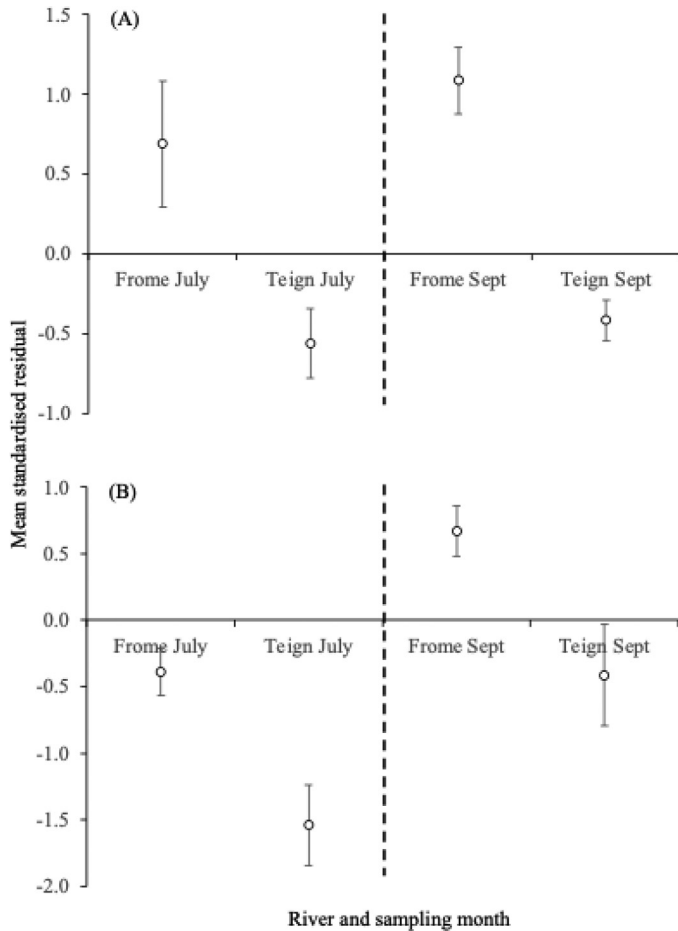


Fig. 2. Mean standardised growth residuals (clear circles) and their 95% CI (vertical lines) of (A) Brown trout and (B) Atlantic salmon for the Rivers Frome and Teign between samples collected in July and September. The dashed line separates the samples collected in July and September. Negative values indicate smaller lengths at the last annulus versus the predicted lengths of the regression model fitted using data from across both rivers and all sampling occasions.

predicted values derived from the model (Beardsley and Britton, 2012). These standardised residuals were then tested between the two rivers using ANOVA, with the mean standardised residuals ($\pm 95\%$ confidence limits) also plotted for comparative purposes (Fig. 2). For salmon, the presence of only 1 yr class present in the Frome meant that rather than plotting lengths at age, length at capture at age 0+ was used across both rivers only, with the mean length of all 0+ fish used to calculate the standardised residuals as outlined above, which were then tested in ANOVA. In all cases, negative standardised residuals from the regression indicate trout with their length at the last annulus being below the predicted length at age fitted by the regression model, and salmon that were smaller than the predicted 0+ fish length (*i.e.*, the growth rates of these fish were slower than predicted by the model).

2.3 Stable isotope analyses

All of the fish fin tissue and macroinvertebrate samples were dried to constant mass at 60 °C within four weeks of

sampling. These samples were then analysed at the Cornell University Stable Isotope Laboratory (New York, USA) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific, USA) interfaced to a NC2500 elemental analyser (CE Elantach Inc., USA), with this completed within six months of the fish being sampled. Analytical precision of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 to 3.9) (Winter and Britton, 2021). As the putative macroinvertebrate prey of the River Frome were all from the same reach and direct comparisons in stable isotope metrics were not being completed with the Teign fish then the Frome SI data were used in their original form. In the River Teign, however, there were temporal and spatial differences in the SI data that meant the fish data were corrected (De Santis *et al.*, 2021). $\delta^{15}\text{N}$ were converted to trophic position (TP) (Olsson *et al.*, 2009):

$$\text{TP} = (\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{prey}} / 3.4) + 2 \quad (1)$$

where TP and $\delta^{15}\text{N}_{\text{fish}}$ are the trophic positions and the nitrogen ratios of each individual fish, $\delta^{15}\text{N}_{\text{prey}}$ is the mean nitrogen ratio of the putative macroinvertebrate prey resources, 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). The $\delta^{13}\text{C}$ data were converted to corrected carbon ($\delta^{13}\text{C}_{\text{corr}}$) (Olsson *et al.*, 2009):

$$\delta^{13}\text{C}_{\text{corr}} = (\delta^{13}\text{C}_{\text{fish}} - \delta^{13}\text{C}_{\text{meanMI}}) / \text{CR}_{\text{MI}} \quad (2)$$

wherein $\delta^{13}\text{C}_{\text{fish}}$ is the $\delta^{13}\text{C}$ value of each fish, $\delta^{13}\text{C}_{\text{meanMI}}$ is the mean $\delta^{13}\text{C}$ of the macroinvertebrate prey and CR_{MI} is the carbon range ($\delta^{13}\text{C}_{\text{max}} - \delta^{13}\text{C}_{\text{min}}$) of the same macroinvertebrates (Olsson *et al.*, 2009). An important aspect in the application of Equation (1) and (2) was the putative prey macroinvertebrate resource data used in the calculations. Sampling of the macroinvertebrates in the focal Teign sites revealed a relatively species poor community of low abundance, where the only taxonomic group sufficiently present to provide at least triplicate samples for SIA across all three sites was *Gammarus pulex*. Thus, it was *Gammarus pulex* that were used exclusively for the macro-invertebrate SI data in Equation (1) and (2). Functionally, gammarids are detritivores that often consume some terrestrial resources, with these resources tending to be less variable between sites than aquatic resources, meaning the full extent of isotopic variability in the putative prey resources might not have been captured (*i.e.*, underestimated). However, MacNeil *et al.* (1997) suggested that *Gammarus pulex* has a wider food base than is often acknowledged, which would increase their isotopic variability and reducing the effect of this limitation on calculations in Equation (1) and (2). In addition, a visual inspection on the original SI data at the species/ site/ date level was also completed to identify whether there were any major discrepancies between the patterns between the original and corrected data that could indicate an issue with the application of these macroinvertebrate data.

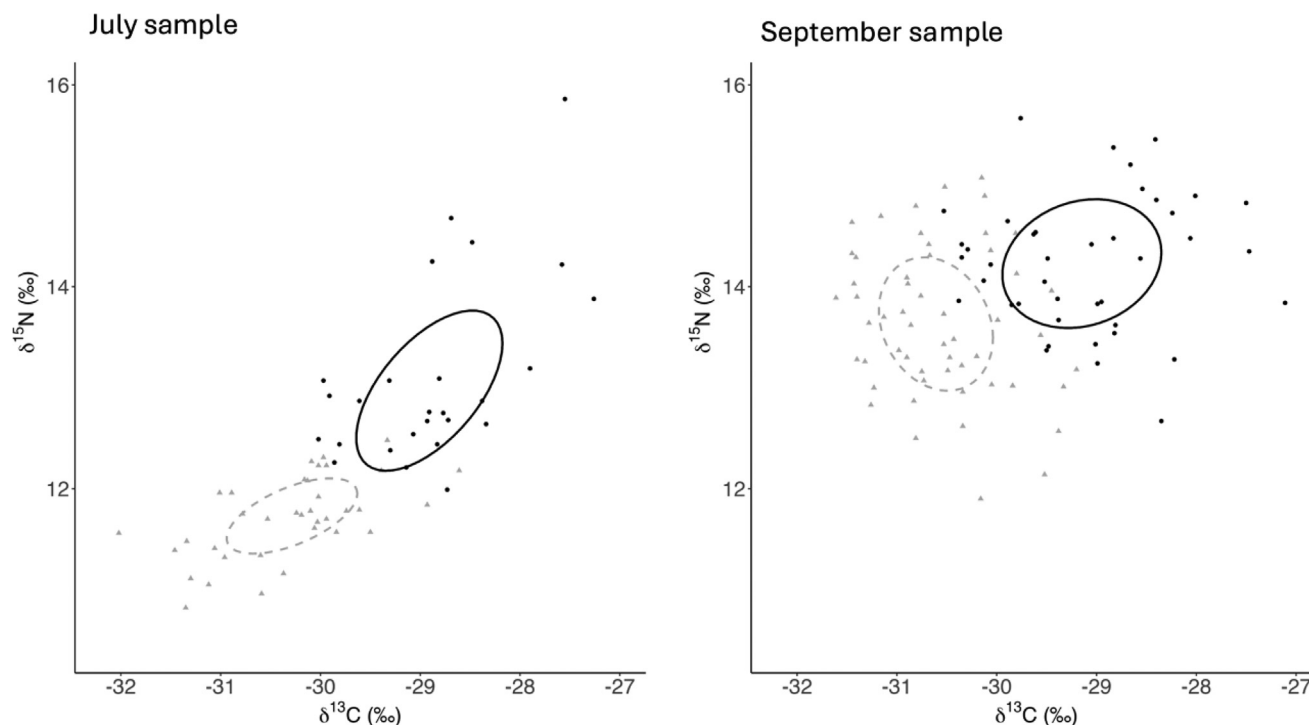


Fig. 3. Standard ellipse areas of sympatric Atlantic salmon (grey ellipse) and brown trout (black ellipse) for samples collected from the River Frome in July and September 2008. Note that these stable isotope data were used without correction.

The fish original SI data for the Frome, and corrected SI data for focal Teign sites were then used to calculate the trophic niche sizes (as the stable isotope niche) of salmon and trout for each location and sampling date (Tab. 1). These calculations used the stable isotope niche as a proxy of the trophic niche (Jackson *et al.*, 2011). Whilst closely related to the trophic niche, the stable isotope 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; Jackson *et al.*, 2012), where SEAs are a bivariate measure of the distribution of individuals in stable isotope 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; Jackson *et al.*, 2012). Differences in the sizes of stable isotope 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 stable isotope niche overlap (%) between the species using SEA_c in SIBER (subscript 'c' indicates a small sample size correction was used; Jackson *et al.*, 2012).

Differences in TP and $\delta^{13}\text{C}_{\text{corr}}$ between the allopatric and sympatric contexts in the River Teign were tested for each species in linear mixed effects models (LMEM), where prior to

model construction, assumptions of normality of residuals and homoscedasticity were checked. The structure of the data used in the model combined the site level data into the two contexts of allopatry and sympatry, with each site within the contexts representing a replicate. Using data from each individual fish per site and per context in the model as true replicates would inflate the residual degrees of freedom and so the models fitted site as a random effect (Dossena *et al.*, 2012). The model structure used TP and $\delta^{13}\text{C}_{\text{corr}}$ as the dependent variable, context and fish length as fixed effects, and site as the random variable. Each model was fitted using restricted maximum likelihood to determine the parameter estimates, with differences in TP and $\delta^{13}\text{C}_{\text{corr}}$ by context determined using estimated marginal means and multiple comparison post-hoc analyses (general linear hypothesis test). The LMEMs were then complemented by calculation of the stable isotope metrics as outlined above.

All data analyses were completed in R Development Core Team, (2022). Where error is provided around mean values, it represents 95% confidence limits unless otherwise stated.

3 Results

3.1 Lengths and growth rates of sympatric salmonids

Salmon present in the River Frome samples were between 60 and 110 mm and between 53 and 147 mm in the Teign (Tab. 1), with the latter being significantly larger ($F_{1,224}=36.57$, $P<0.001$). Trout in the River Frome samples were between 73 and 361 mm versus 48 and 325 mm in the Teign (Tab. 1), with these differences not significant (ANOVA: $F_{1,239}=0.22$, $P=0.64$). All Frome salmon were age 0+ at the

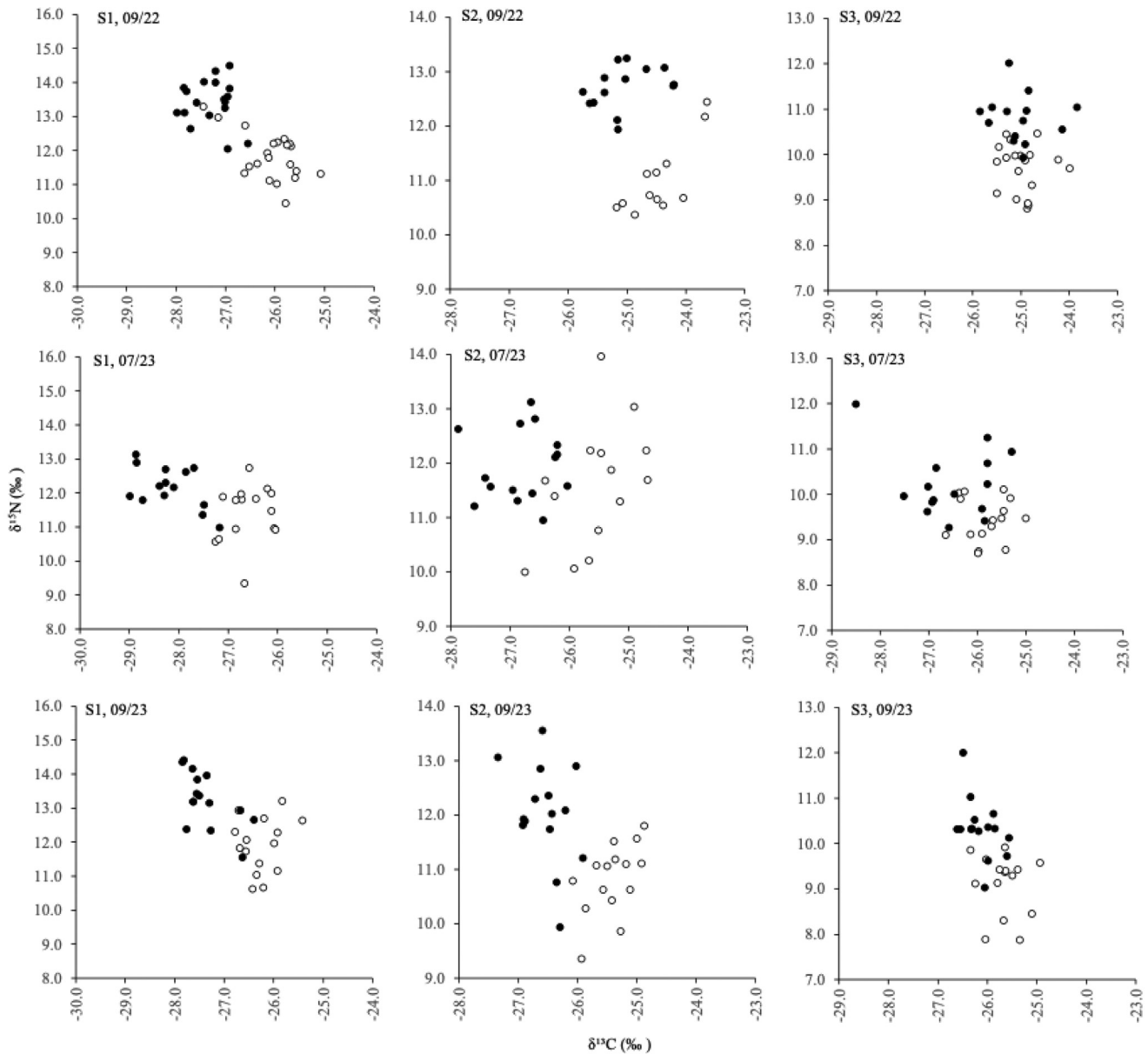


Fig. 4. Stable isotope plots (using uncorrected values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of Atlantic salmon (filled circles) and brown trout (clear circles) for Site (S) 1, 2 and 3 in September (9) 2022 and 2023, and July (7) 2023. Note the differences in scales on the x and y axes for the plots between S1 to S3, which was done data comparison purposes between the two species.

time of sampling versus between 0+ and 2+ in the Teign, whereas trout in both rivers were present between age 0+ and 3+. The standardised residuals of the lengths at the last annulus of Teign trout, and of 0+ salmon length, were all negative (*i.e.*, slower growing than predicted), whereas both metrics for the Frome in September were positive (*i.e.*, faster growing than predicted), with these growth differences being significant (ANOVA: trout $F_{3,209} = 55.72, P < 0.001$; salmon $F_{3,126} = 26.55, P < 0.001$; Fig. 2).

3.2 Stable isotope analyses of sympatric salmonids

The relationships between fish length and $\delta^{13}\text{C}$, $\delta^{13}\text{C}_{\text{corr}}$, $\delta^{15}\text{N}$ and TP were generally significant for each species and

river, except Teign trout versus TP and Frome salmon versus $\delta^{13}\text{C}$ (Tabs. 1 and 2). In all significant regressions, the relationship between length and the stable isotope metric was positive, with increasing values of $\delta^{13}\text{C}$, $\delta^{13}\text{C}_{\text{corr}}$, $\delta^{15}\text{N}$ and TP as length increased. The stable isotope metrics for salmon and trout in the River Frome revealed a consistent pattern of trophic niche partitioning between the species in samples collected in both July and September, with no overlap in standard ellipse areas (Tab. 1; Fig. 3). The general patterns observed in the uncorrected data in the focal Teign sites were broadly similar to those of the corrected data (Figs. 3 and 4). The corrected data enabled appropriate comparison in isotopic niche metrics between the species and sites, with trout and salmon in Sites 1 and 2 being

Table 2. Results of linear regression testing the relationship of fish length versus stable isotope values and metrics, where *significant relationship ($P \leq 0.05$).

River	Species	Isotope	Regression output
Frome	Salmon	$\delta^{13}\text{C}$	$R^2 = 0.03$; $F_{1,89} = 2.97$, $P = 0.88$
	Salmon	$\delta^{15}\text{N}$	$R^2 = 0.30$; $F_{1,89} = 37.28$, $P < 0.001^*$
	Trout	$\delta^{13}\text{C}$	$R^2 = 0.51$; $F_{1,95} = 101.61$, $P < 0.001^*$
	Trout	$\delta^{15}\text{N}$	$R^2 = 0.43$; $F_{1,95} = 70.40$, $P < 0.001^*$
Teign	Salmon	$\delta^{13}\text{C}_{\text{corr}}$	$R^2 = 0.03$; $F_{1,233} = 3.95$, $P = 0.05^*$
	Salmon	TP	$R^2 = 0.04$; $F_{1,233} = 4.92$, $P = 0.03^*$
	Trout	$\delta^{13}\text{C}_{\text{corr}}$	$R^2 = 0.24$; $F_{1,140} = 46.58$, $P < 0.001^*$
	Trout	TP	$R^2 = 0.01$; $F_{1,140} = 0.01$, $P = 0.95$

Table 3. Location (as latitude/ longitude), sample sizes (n) by site and species for the allopatric Atlantic salmon *Salmo salar* ("salmon") and brown trout *Salmo trutta* ("trout"), their mean fork length ("length"), mean stable isotope data (as $\delta^{13}\text{C}$ or $\delta^{13}\text{C}_{\text{corr}}$ (Eq. (2)) and $\delta^{15}\text{N}$ or trophic position (TP; Eq. (1)). All values in parentheses are standard deviation (cf. Tab. 5, Fig. 5 for isotopic niche metrics).

Species	Site n	Location	Sample n	Length (mm)	$\delta^{13}\text{C}_{\text{corr}}$ (‰)	TP
Allopatric salmon	4	50.67338, -3.65241	11	96 (19)	0.49 (0.14)	3.69 (0.18)
	5	50.69552, -3.78101	8	84 (17)	0.77 (0.29)	3.96 (0.10)
	6	50.70006, -3.77791	14	70 (9)	0.37 (0.35)	3.91 (0.08)
Allopatric brown trout	7	50.52554, -3.62559	16	159 (28)	1.36 (0.26)	3.36 (0.12)
	8	50.60817, -3.71207	15	103 (19)	1.43 (0.21)	3.44 (0.10)
	9	50.59468, -3.61571	11	127 (22)	1.10 (0.42)	3.45 (0.10)
	10	50.56380, -3.69157	15	97 (15)	1.54 (0.43)	3.43 (0.12)

strongly divergent in their trophic niches, with similar niche positions and sizes in both species on all sampling occasions (Tab. 1; Figs. 4 and 5). In Site 3, the trophic niches of the two species less diverged, but still had relatively limited overlap (Figs. 4 and 5).

3.3 Stable isotope analyses of salmonids in allopatry vs sympatry

The LMEMs revealed that in both brown trout and salmon, differences in TP and $\delta^{13}\text{C}_{\text{corr}}$ were not significant between allopatry and sympatry in the River Teign, with fish length being the only significant variable for $\delta^{13}\text{C}_{\text{corr}}$ in both species (Tabs. 3 and 4). Moreover, comparison of the stable isotope niche positions of the allopatric and sympatric contexts by species revealed that their overall niche positions in stable isotope space were relatively similar between the two contexts. For the isotopic niche, SEAc indicated larger niche sizes in sympatry, but with the 95% credible intervals of SEA_B overlapping between the contexts for both species (Tab. 5). Within each species, there was relatively high niche overlap at allopatric versus sympatric contexts (>90%; Fig. 6; Tabs. 3 and 5).

4 Discussion

The sympatric brown trout and Atlantic salmon populations of these two rivers in Southern England revealed consistent patterns of stable isotope niche partitioning. The

positions of the stable isotope niches of trout and salmon were similar in both allopatry and sympatry and, while the singular estimates of the standard ellipse areas (SEA, SEAc) indicated larger niche sizes in sympatry, the 95% credible intervals of SEA_B indicated these niches did overlap in their sizes. Accordingly, with the minimal differences in niche position and overlaps in the 95% credible intervals of SEA_B suggest alignment to the niche conservation hypothesis, with the species in allopatry not consuming a wider range of prey resources than those in sympatry. This pattern of stable isotope niche partitioning is consistent with some other salmonid fish communities, such as coexisting brown trout, Arctic charr *Salvelinus alpinus* and brook trout *Salvelinus fontinalis* (Eloranta *et al.*, 2013; Cucherousset *et al.*, 2007).

The standardised growth residuals of both salmonid species indicated relatively slow growth in the River Teign, with some salmon being in their third year of life without yet running to sea as smolts, whereas most salmon in the Frome emigrate to sea at age 1+ years (Simmons *et al.*, 2020, 2022). Although prey availability was not measured quantitatively in either the Frome or Teign, the Frome and its connected side-streams are recognised for their high macroinvertebrate diversity and abundances, with it being a chalk stream of high water quality (Cannan and Armitage, 1999; Armitage *et al.*, 2003). The Teign is comparatively species poor compared to the Frome and has generally lower macroinvertebrate abundances, but also has high water quality in the study reaches (Gravelle *et al.*, 1997). Despite the suggested lower productivity in the Teign versus the Frome, there was no evidence to suggest the two salmonid fishes were competing

Table 4. Results of general linear mixed models testing differences trophic position and $\delta^{13}\text{C}_{\text{corr}}$ between allopatry and sympatry (“Context”) for brown trout (BT) and Atlantic salmon (AS), where fish length (“L”) was included as a fixed factor and site was the random variable.

Species	Coefficient	<i>F</i>	<i>P</i> -value
BT ~ TP	(Intercept)	1187.29	<0.001
	Context	0.26	0.61
	L	3.10	0.08
BT ~ $\delta^{13}\text{C}_{\text{corr}}$	(Intercept)	5.80	0.05
	Context	2.24	0.14
	L	41.76	<0.001
AS ~ TP	(Intercept)	643.87	<0.001
	Context	0.01	0.91
	L	0.01	0.94
AS ~ $\delta^{13}\text{C}_{\text{corr}}$	(Intercept)	0.09	0.78
	Context	0.01	0.99
	L	4.10	0.05

Table 5. Stable isotope niche metrics for allopatric and sympatric populations of Atlantic salmon and brown trout in the Teign where length: mean fork length ($\pm 95\%$ CI), TA: the total area of the convex hull encompassing the data points, SEA: the Standard Ellipse Area containing 40% of the data, SEA_C : Correction applied to SEA to account for small sample sizes, and the Bayesian estimate for SEA (SEA_B) expressed as their 95% credible intervals.

Context	Species	N	Length (mm)	$\delta^{13}\text{C}_{\text{corr}}$	Trophic position	TA	SEA	SEA_C	SEA_B (95%CI)
Sympatric	Salmon	45	99 (4)	0.56 (0.1)	3.78 (0.1)	2.39	0.63	0.64	0.46 – 0.84
	Trout	45	135 (8)	1.51 (0.1)	3.41 (0)	2.09	0.62	0.63	0.45 – 0.82
Allopatric	Salmon	33	82 (5)	0.43 (0.1)	3.82 (0)	1.31	0.39	0.40	0.27 – 0.54
	Trout	57	122 (6)	1.37 (0.1)	3.42 (0.1)	2.32	0.44	0.44	0.33 – 0.57

for shared prey resources in the Teign. The partitioning in their stable isotope niches indicated some differentiation in their resource use, with presumably sufficient prey diversity and abundance in the river to support both fish populations (MacArthur, 1965; Ross, 1985). Nevertheless, a limitation of the study here was its inability to develop greater understandings in the differences in resource use between the two species in the Teign (as the less productive system), at least in part to the low taxonomic diversity that was captured in the macroinvertebrate samples. This resulted in the sole use of gammarids as putative prey resources in Equation (1) and (2), which has already been outlined as a limitation due to their detritivory of allochthonous terrestrial resources (*cf.* Methods and Materials). Although the datasets for two rivers were collected approximately 15 yr apart, this was not considered a limitation due to the stable isotope processing occurring in the following months after sampling. However, these results do indicate that to understand the differences in prey between the species would need to use complementary methods such as stomach content analyses (Amundsen and Sánchez-Hernández, 2019) and/or DNA based approaches (Traugott *et al.*, 2021).

When species are present in allopatric contexts then the lack of inter-specific competition can enable the population to exploit a wider range of resources versus their populations within communities where other species are present, with allopatric diets thus often being more generalised than those in sympatry (Tran *et al.*, 2015). This was not, however, evident in the River Teign, where the stable isotope values and niche sizes

and positions of the allopatric trout and salmon were similar to those in sympatry – and where there were differences in metrics (*e.g.*, SEA_C), they indicated larger niches in sympatry than allopatry. Where niche sizes are larger in sympatry, it suggests some intra-specific resource partitioning and/or greater opportunistic foraging in the presence of another salmonid fish. While not tested directly, the stable isotope niche partitioning evident between the two species in sympatry was interpreted as being due to some subtle differences in their functional morphologies and habitat use, which were then conserved when the fish were in allopatry, with this retention of their trophic niche characteristics across these contexts being consistent with the niche conservation hypothesis (Comte *et al.*, 2017). These salmonid populations were thus consistent with other communities of sympatric salmonids that often exhibit strong ecological and trophic niche partitioning (Eloranta *et al.*, 2013). This has already been detected in lake dwelling populations of salmon and trout where dietary specialisations were enabled through piscivory (Jørgensen *et al.*, 2000). In stream populations, the more limited space available to the fishes potentially increases the potential for niche overlap to occur, and thus the differences in habitat use that generally occur between these species (*e.g.*, juvenile salmon use faster flowing and shallower habitats versus trout) were assumed as being an important factor in driving this niche conservatism (Heggenes *et al.*, 1999).

The coexistence of fishes can, however, be driven more by differences in their dietary resource use rather than habitat

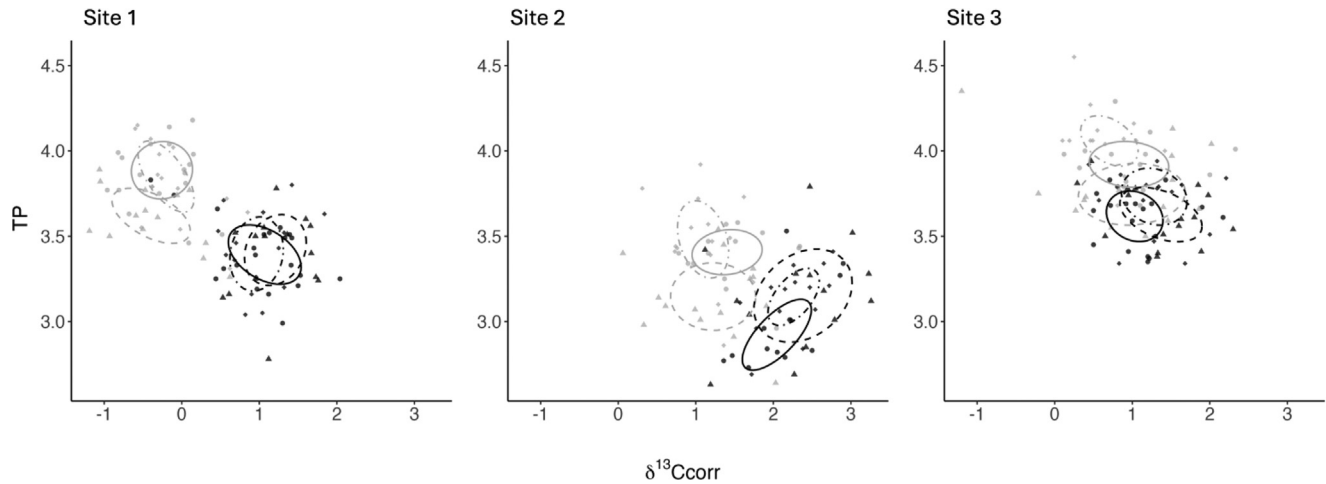


Fig. 5. Stable isotope niches using corrected stable isotope data ($\delta^{13}\text{C}$ to $\delta^{13}\text{C}_{\text{corr}}$ (‰); Eq. (2); $\delta^{15}\text{N}$ to trophic position (TP); Eq. (1) for Atlantic salmon (grey ellipses) and brown trout (black ellipses) in the River Teign sites (*cf.* Tab. 1 details and sample sizes, Fig. 3 for uncorrected data), where solid lines are fish sampled in September 2022, long dashes in July 2023 and short dashes in September 2023.

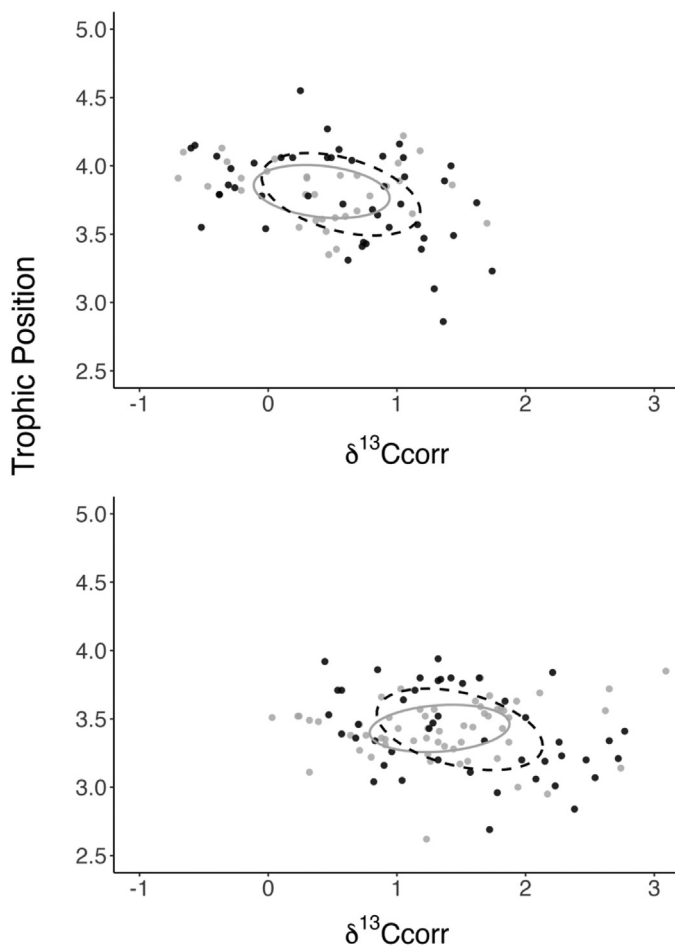


Fig. 6. Stable isotope niches according to $\delta^{13}\text{C}_{\text{corr}}$ (‰; Eq. (2) and trophic position (TP; Eq. (1) of Atlantic salmon (top) and brown trout (bottom) in allopatry (grey ellipse) and sympatry (black dashed ellipse) in the River Teign (*cf.* Tab. 3 for sample sizes and fish lengths).

selection (Ross, 1986), where interspecific stable isotope niche partitioning reduces the competitive interactions between species by promoting niche complementarity (Larocque *et al.*, 2020). Within salmonids, rainbow trout *Oncorhynchus mykiss* and brook trout can shift their diets towards resources of higher $\delta^{13}\text{C}$ values as they grow (Ciancio Blanc *et al.*, 2008; Jardine *et al.*, 2005), with this ontogenetic diet shift often representing a shift from aquatic to terrestrial prey, and thus this diversification of diet reduces the intensity of competition for aquatic prey resources (Sánchez-Hernández and Cobo, 2018). In addition, the competitive interactions and trophic relationships of populations of coexisting salmonid fishes potentially influences the expression of their life history strategies (Simmons *et al.*, 2022). In both rivers, salmon are considered to express obligate anadromy, where the only major difference between the rivers was their age of emigration, with this influenced by their somatic growth rates and thus, most likely, differences in prey abundances or fish density, but not the trophic niche size or position of the population, or the niche overlap with trout. The brown trout populations of both rivers express facultative anadromy, where within populations, some individuals express anadromy and others remain as river residents (Jonsson and Jonsson, 2021). However, the results present here do not provide evidence that the decision of whether to stay within the river or to emigrate to sea was driven by issues relating to their trophic niche size, position or overlap with salmon (Ferguson *et al.*, 2019).

In conclusion, despite contrasting somatic growth between these salmonid fish populations across the two rivers, the general patterns detected in their stable isotope niches were similar, with stable isotope niche partitioning evident and with these niches being largely conserved when the species were in allopatry. These results suggest that differences in individual and population level growth rates were not important factors in driving their trophic niche sizes and were considered to instead relate to differences in functional morphology and habitat use. These results thus emphasise the importance of identifying the differences in trophic ecology between closely related

coexisting fish species for developing new understandings of their inter-specific interactions.

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