

ORIGINAL ARTICLE

Seasonal trophic niche width and overlap of mottled sculpin and brown trout in a regulated high-elevation river

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Abstract

In temperate ecosystems, resource availability fluctuates seasonally due to changes in environmental conditions and productivity. Intra- and inter-specific trophic niche overlap under resource limitation is a measure of competitive interactions and influences species coexistence and community dynamics, but patterns of this overlap are influenced by anthropogenic activities. To investigate seasonal trophic niche dynamics of coexisting fish species in a flow-altered river, we analysed prey resources, stomach content samples and stable isotope signatures of mottled sculpin *Cottus bairdii* and juvenile brown trout *Salmo trutta* in the Blue River, Colorado, USA, a high-elevation oligotrophic river. Prey biomass (i.e. benthic macroinvertebrates) peaked in spring and declined through summer and autumn. Stomach content and stable isotope analysis results showed that diet composition of mottled sculpin and brown trout varied seasonally in response to changes in prey availability. Stomach content analysis results revealed that in autumn, both species exhibited the highest frequency of empty stomachs and expanded population trophic niches due to increased inter-individual diet variation despite decreased individual trophic niche breadth. Inter-specific trophic niche overlap was relatively high across all seasons, but the lowest degree of overlap occurred in autumn of both years when prey availability was lowest. Isotopic analysis revealed similar trends to stomach content analysis, of wider isotopic niches and reduced overlap in autumn compared to spring. Our data indicated that seasonal variation affected individual- and population-level trophic niche dynamics and inter-specific niche overlap between mottled sculpin and brown trout. This trophic segregation under resource limitation may serve as a mechanism that facilitates species coexistence in a flow-regulated, oligotrophic river.

KEYWORDS

coldwater rivers, fish diet, flow alteration, resource partitioning, sympatric species, trophic niche

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1 | INTRODUCTION

Knowledge on intra- and inter-specific niche overlap is paramount to understanding dynamics of stream populations and communities (Bolnick et al., 2002; Durbec et al., 2010; Larocque et al., 2021) and the structure of stream ecosystems (Araújo et al., 2011; Maitland & Rahel, 2023; Mason et al., 2008). Individual variation in ecological niche space can be high in lotic organisms (Bolnick et al., 2007; Jirka & Kraft, 2017) and the degree of intra-specific niche variation has been used to quantify ecological and evolutionary capacities of species to adapt to environmental change (Bolnick et al., 2002; Brazil-Sousa et al., 2023). Niche overlap between species can lead to the extirpation of a less competitive species (Bøhn et al., 2008; Gause, 1934; Hardin, 1960). Characterizing both intra- and inter-specific niche overlap is needed to predict species coexistence (Da Silva et al., 2017; Durbec et al., 2010), where stronger intra-specific niche overlap relative to inter-specific overlap facilitates the coexistence of ecologically similar species (Chesson, 2000). Intra- and inter-specific niche overlap changes over time in seasonal streams, where resource availability varies with shifts in environmental conditions and productivity throughout the year (Falke et al., 2020; Marcarelli et al., 2020; Neves, Costa-Pereira, et al., 2021; Neves, Kratina, et al., 2021). Quantifying this temporal pattern is becoming more important in stream fish management because anthropogenic disturbances such as dams and climate change are shifting the seasonality and phenology of lotic ecosystems (Poff et al., 1997; Staudinger et al., 2021).

Trophic niche width reflects the range of resources an individual or population uses and can expand or contract in response to resource availability and the relative intensity of intra- and inter-specific competition (Araújo et al., 2011; De Santis et al., 2021; Roughgarden, 1972). A population's niche width can expand through three primary mechanisms: (1) individuals adopt a more generalist foraging strategy (i.e. individual niche expansion), (2) individuals specialize on different resources, reducing niche overlap within the population (between-individual variation) or (3) a combination of both (Bolnick et al., 2010; Liang et al., 2020; Sargeant, 2007). The release from inter-specific competition is predicted to lead to population niche expansion, either through increased individual niche breadth (parallel release hypothesis) or increased between-individual variation (niche variation hypothesis) (Bolnick et al., 2010; Van Valen, 1965). Both processes of niche expansion following the release from inter-specific competition have been observed across various studies (Costa-Pereira et al., 2017; Hammerschlag et al., 2010; Sánchez-Hernández et al., 2021). Conversely, when resources are limited, sympatric species are expected to diverge in resource use, often through niche contraction, to minimize niche overlap and inter-specific competition (MacArthur & Levins, 1967; Neves, Kratina, et al., 2021; Tran et al., 2015).

Similar niche divergence can occur within a species when competition intensifies due to high population densities and resource

limitation. Here, increased intra-specific competition is associated with increased individual specialization and population niche expansion (Araújo et al., 2008; Svanbäck & Bolnick, 2007). In this context, niche expansion results from greater trophic niche partitioning among individuals within the population (between-individual variation), even when individual niches contract. Despite the growing body of research in this area, patterns of inter- and intra-specific trophic niche dynamics in relation to resource availability exhibit significant variation among different regions and aquatic communities (Flood et al., 2023; Kornis et al., 2020).

This knowledge gap is particularly evident in flow-regulated rivers. Dams have caused widespread alterations to river flows, and these alterations are likely to continue as water development projects occur globally as a climate change adaptation strategy. Yet, our understanding of how fish populations respond to these changes at individual and population scales remains limited (Freeman et al., 2022). Here, we studied mottled sculpin (*Cottus bairdii*) and brown trout (*Salmo trutta*), two fish species that coexist in many coldwater streams throughout North America (Becker, 1983). Although sculpin are often considered potential prey for trout (Meredith et al., 2015), sculpin and juvenile trout share similar niches (Gabler & Amundsen, 1999; Hesthagen et al., 2004; Louhi et al., 2014) and dietary preferences, including benthic macroinvertebrates and other small prey items (Becker, 1983). Despite their prevalence and niche overlap, few studies have evaluated how seasonal resource availability affects trophic dynamics of brown trout and mottled sculpin in flow-regulated rivers. (Larocque et al., 2021).

In this study, we used stomach content analysis (SCA) and stable isotope analysis (SIA) to evaluate seasonal trophic niche dynamics of mottled sculpin and juvenile brown trout in the Blue River, an oligotrophic and regulated river located in north-central Colorado, USA. Both SCA and SIA are common methods in trophic niche and food web studies. On one hand, SCA offers a snapshot of diet composition at the time of sampling and provides a higher level of taxonomic resolution (Nielsen et al., 2018). On the other hand, SIA reflects the assimilation of resources into an organism's tissue over time (weeks or months) and offers a more time-integrated representation of an organism's niche (Matley et al., 2016; Thomas & Crowther, 2015). Therefore, we chose to use a combination of SCA and SIA to gain a more comprehensive understanding of temporal variations in trophic dynamics of mottled sculpin and juvenile brown trout. We tested the following predictions in this study: (1) the study species' trophic niches would shift quantitatively (feeding intensity) and qualitatively (diet composition) in response to changes in resource availability; (2) limited resource availability would promote individual diet specialization and variation among individuals and (3) consequently, limited resource availability would lead to population-level trophic niche expansion and increased trophic niche overlap between the two species.

2 | MATERIALS AND METHODS

2.1 | Study system

The Blue River is a Rocky Mountain stream in north-central Colorado, USA, and is a tributary of the Colorado River. It originates in the Tenmile Range (3900m elevation) and has a watershed area of 1800km². The Blue River is approximately 105 km long and 31 m wide on average under base flow conditions in our study area. This region experiences a temperate climate with seasonal variation in temperature (annual mean: 4.6°C) and precipitation (annual mean: 517 mm). There are two large, hypolimnetic release dams on the Blue River upstream of the study area: Dillon Dam (surface area: 13.1 km²; volume: 0.32 km³) and Green Mountain Dam (surface area: 8.6 km²; volume: 0.19 km³). These dams serve multiple purposes including supplying municipal and irrigation water to local communities, generating hydroelectric power and diverting water to the eastern slope of the Rocky Mountains. The dams have trapped nutrients, resulting in oligotrophic conditions downstream of the impoundments (Bauch et al., 2014), and have also altered the thermal and flow regimes of the river (Figure S1), resulting in temporal variation in resource availability.

Compared to the Eagle River (a nearby unregulated reference stream), the Blue River experiences similar mean daily flows (2021: Blue=7.1 m³/s, Eagle=7.06 m³/s; 2022: Blue=6.7 m³/s, Eagle=9.7 m³/s), however, their seasonal flow patterns are markedly different. During early summer months (May–July), the Blue River experiences low flows compared to the Eagle River (2021: Blue=5.5 m³/s, Eagle=18.4 m³/s; 2022: Blue=3.0 m³/s, Eagle 27.8 m³/s). While in early autumn (August–October) the trend reverses and the Blue River exhibits peak flows that are higher than those of the Eagle River (2021: Blue=11.1 m³/s, Eagle=4.1 m³/s; 2022: Blue=11.8 m³/s, Eagle=4.4 m³/s). The Blue River also experiences a generally cooler and more stable thermal regime compared to the Eagle River (2021: Blue=1.9–13.1°C, Eagle=0–20.8°C; 2022: Blue=1–12.7°C, Eagle=0–20.4°C), due to dams releasing hypolimnetic water. In our study area, brown trout and mottled sculpin are the two predominant fish species, and rainbow trout (*Oncorhynchus mykiss*) are occasionally observed.

Two additional unique aspects of this study merit mention. First, ecological restoration via nutrient addition is being planned in the Blue River. To effectively monitor the ecological response to this restoration effort, baseline data were needed, which we report here. Second, a recent genetic study suggests that there may be more than a single sculpin species in the Colorado River basin (Young et al., 2022). Even if taxonomic uncertainties remain in the mottled sculpin complex, our population is located at the southern edge of their native range in a high-elevation river and provides key ecological information to characterize their diversity. Our current study was motivated by these unique taxonomic, ecological and conservation contexts.

2.2 | Field sampling

Sampling was conducted at five sites, each approximately 100 metres in length, along a 4 km stretch of the Lower Blue River, in spring (May), summer (August), and autumn (October) of 2021 and 2022. Our goal was to focus on juvenile brown trout (80–200 mm) and mottled sculpin (80–135 mm). This size range aimed to capture sexually immature brown trout, as they typically reach 80 mm in their first year and achieve sexual maturity around 200 mm (Pavlov et al., 2020; Taube, 1976). Data on sculpin maturity in our region are limited, but research suggests females exceeding 40 mm are likely mature (Grossman et al., 2002; Patten, 1971). The largest sculpin observed in our study was 135 mm.

Fish were collected along the margins of the river, using a three-pass removal method with backpack electrofishers (Smith-Root Model LR-24; Vancouver, WA, USA). To estimate fish abundance, we calculated catch-per-unit-effort (CPUE) based on the average number of fish per square meter (fish/m²) caught during the first pass at each site during each sampling occasion. We chose to calculate CPUE based on fish from the first pass because we did not use blocknets to prevent fish movement, which likely violated the assumption of a closed population required for depletion methods. CPUE changed over time due partly to catch efficiency at different flows. Brown trout (80–200 mm) had a CPUE range of 0.02–0.07 fish/m² (mean: 0.04) across sampling occasions, and mottled sculpin (80–135 mm) had a CPUE range of 0.02–0.04 fish/m² (mean: 0.03).

All captured fish from the three electrofishing passes were measured (brown trout with fork length [FL] and mottled sculpin with total length [TL]; to the nearest mm) and weighed (to the nearest g). A minimum of 30 fish within our size range (brown trout: 80–200 mm; mottled sculpin: 80–135 mm) were targeted for stomach content analysis. If the target number was not collected during the initial three passes, additional sampling was performed. Fish meeting the target size range were anesthetized (AQUI-S®, Lower Hutt, New Zealand) and gastrically lavaged to collect stomach content samples. Of these sampled fish, 15 individuals per species, varying in size, were sacrificed for stable isotope analysis using an overdose of AQUI-S. Stomach content samples and sacrificed fish were placed on ice in the field and subsequently frozen at the laboratory until they were processed.

To evaluate seasonal variation in resource availability for fish, benthic macroinvertebrates (BMI) were sampled within 1–2 weeks of our fish sampling events (except for autumn of 2022 when sampling did not occur). At each sample site, three random samples were collected from both the top and bottom of the reach using a Surber sampler (500 µm net; 0.09 m²). These samples were pooled (one for top reach and one for bottom reach) and subsequently sent to the Aquatic Biology Associates (Corvallis, OR, USA) for identification, and abundance and biomass estimates (using length-mass conversion equations; Benke et al., 1999).

2.3 | Laboratory sample preparation and processing

2.3.1 | Stomach content analysis

Stomach content analysis was performed on 827 brown trout and 758 mottled sculpin. Prey were identified to the lowest taxonomic level possible (Family or Order, depending on the level of digestion) using a dissecting microscope. Body length or head capsule width of each prey item was measured to the nearest 0.1 mm and then converted to whole-body dry mass estimates using length-mass relationships (Benke et al., 1999; Collins, 1992; Sabo et al., 2002). Prey were then categorized into 14 different groups: (1) Ephemeroptera larvae, (2) Plecoptera larvae, (3) Trichoptera larvae, (4) Diptera larvae, (5) Coleoptera larvae, (6) Coleoptera adults, (7) Gastropoda, (8) Amphipoda, (9) Isopoda, (10) Oligochaeta, (11) Emergent aquatic insects, (12) Terrestrial insects, (13) Salmonidae or (14) Other. The 'Other' group consisted of prey items that represented less than 1% of the dry mass in stomachs of brown trout or mottled sculpin in any given sampling occasion. Diet composition for each individual fish was characterized as the proportional dry mass of prey groups present in relation to total stomach content dry mass.

2.3.2 | Stable isotope analysis

For stable isotope analysis, a skinless and boneless dorsal muscle tissue sample was collected from each sacrificed fish and dried at 60°C for a minimum of 72 h or until dry weight stabilized. Desiccated samples were ground to a homogeneous powder using a mortar and pestle, which were cleaned with ethanol between samples to avoid cross-contamination. Samples were then sent to the Cornell University Isotope Laboratory (Ithaca, NY, USA) where they were encapsulated and analysed for elemental percentage of N (%N) and C (%C), and the corrected isotope delta value for ^{15}N ($\delta^{15}\text{N}$) and ^{13}C ($\delta^{13}\text{C}$) in parts per mil (‰) (Fry, 2006). The analyses were performed using a model NC2500 elemental analyser (Carlo Erba, Milan, Italy) interfaced to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer (Thermo Fisher Scientific, Bremen, Germany). The standard for $\delta^{13}\text{C}$ values was Vienna Pee Dee Belemnite and the standard for $\delta^{15}\text{N}$ values was atmospheric air. Internal standards were analysed after every 10 samples to maintain instrument accuracy and precision. The SD of isotopic measurements of standards was 0.08‰ for $\delta^{15}\text{N}$, and 0.11‰ for $\delta^{13}\text{C}$. Data were not lipid normalized because the mean C:N ratio was 3.25 (SD: 0.11); for brown trout and 3.36 (SD: 0.09) for mottled sculpin, and 95% of the C:N ratios were below the standard lipid correction threshold of 3.5 C:N (Skinner et al., 2016).

2.4 | Data analysis

2.4.1 | Prey availability (benthic macroinvertebrates)

To evaluate whether resource availability (BMI biomass) varied seasonally, we fit an ANOVA, with season as the predictor variable and BMI biomass as the response variable, followed by Tukey's HSD test for pairwise comparisons. Sites were pooled because we found no significant effect of site on BMI biomass ($F=0.34$, $p=.85$).

2.4.2 | Stomach content analysis

Feeding intensity

Vacuity index (VI) and stomach fullness index (SFI) were used to evaluate seasonal variation in feeding intensity. Vacuity index (VI) is a measure of the percentage of empty stomachs. Stomach fullness index (SFI) is a measure of how much food an individual has eaten relative to their weight. A generalized linear mixed model and a linear mixed model were fit using %VI and log-transformed SFI as the response variables respectively (*glmer* and *lmer* functions in the *lme4* package; Bates et al., 2015). The models included season and year as fixed effects, and sample site as a random effect. Seasonal differences in %VI and SFI for brown trout and mottled sculpin were compared using Tukey-adjusted pairwise comparisons.

Prey selectivity

To evaluate prey selectivity of mottled sculpin and juvenile brown trout across seasons, we used Vanderploeg and Scavia's relativized electivity index based on the mean proportion of prey groups in the population's diet and their proportions in the environment (BMI biomass) (Chesson, 1978; Vanderploeg & Scavia, 1979). Prey groups found in fish diets but not represented in BMI community data (or vice versa) were excluded from the analysis. Electivity values range from -1 to 1, where 0 indicates prey are being consumed in proportion to their availability in the environment, values less than -0.3 indicate avoidance, and greater than 0.3 indicate positive selection.

Individual & population trophic niches

To evaluate seasonal variation in resource use, we quantified trophic niche width of populations, as well as individual specialization within each population. Total trophic niche width (TNW) reflects the range of prey consumed by a population, and is composed of: (1) within individual component (WIC), a measure of the average niche width of individuals within a population, and (2) between individual component (BIC), a measure of the variation in niche positions between

individuals (Roughgarden, 1972). Their ratio (WIC/TNW) reflects an individual's niche width in relation to the niche width of the whole population and is a measure of individual specialization within a population (Bolnick et al., 2002). Smaller WIC/TNW values suggest individuals with more specialized diets, while larger WIC/TNW values suggest individuals with more generalist diets. These metrics were based on dry mass values of the prey groups and calculated using the WTdMC function in the *RinSp* package (Zaccarelli et al., 2022). We calculated prey proportions in individual diets and then averaged them to reduce the influence of individuals consuming large prey items (Zaccarelli et al., 2022). Monophagous individuals (diet composed of one prey type) can bias results, drawing WIC values down to 0 (Zaccarelli et al., 2022). To address this, we calculated WIC values both with and without monophagous individuals. We found no clear differences, and therefore opted to include monophagous individuals and did not change the weighting of individuals.

Inter-specific trophic niche overlap

Seasonal trophic niche overlap between brown trout and mottled sculpin was estimated using Schoener's index of overlap, which compares the average proportion of prey groups consumed by both species (Schoener, 1970). The index ranges from 0% to 100%, with 0% indicating no overlap and 100% indicating complete overlap. A value of 60% or greater is considered to show significant diet overlap (Zaret & Rand, 1971).

Diet composition

Differences in diet composition were tested using a permutational multivariate analysis of variance (PERMANOVA; *adonis2* function in the *vegan* package; Oksanen et al., 2022). PERMANOVA is a non-parametric version of the multivariate analysis of variance (MANOVA), which allows for comparisons between groups with multiple response variables, such as diet composition. Species, season, year, sample location and an interaction between species and season were included as fixed effects. The PERMANOVA was performed with 9999 permutations and was based on a Bray-Curtis similarity matrix, with prey dry mass data transformed to the fourth root to minimize the influence of extreme prey weights (*metaMDS* function in the *vegan* package). A pairwise PERMANOVA was then used to test for significant differences between species and seasons (*permanova_pairwise* function in the *ecole* package; Smith, 2021). We did not find significant body-size-related differences in diet composition (Table S3) likely because we targeted a relatively narrow range of body sizes in this study. Therefore, individuals of all sizes were grouped for each species, season and year. It should be noted that PERMANOVA tests are sensitive to differences in group dispersion (Anderson, 2001; Warton et al., 2012). Therefore, when significant differences between groups were found, homogeneity of multivariate dispersion was assessed (PERMDISP; *betadisper* function in the *vegan* package). If differences in group dispersion were detected, corresponding non-metric multidimensional scaling (NMDS) plots were evaluated to determine whether differences in groups were solely related to

dispersion or both dispersion and centroid location (Bakker, 2023). NMDS is an ordination technique that uses a similarity matrix to visualize pairwise distances between observations, which provides information on the relationships between groups (dispersion and centroid location). A similarity percentage analysis, with 9999 permutations, was then used to identify prey groups that contributed to differences in diets (SIMPER; *simper* function in the *vegan* package). NMDS and SIMPER were conducted using the Bray-Curtis similarity matrix.

2.4.3 | Stable isotope analysis

Isotopic composition

Differences in mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were used to assess seasonal variation in the prey sources and trophic levels of brown trout and mottled sculpin. Linear mixed models were fit to the data, with species, season, year and the interaction between species and season as fixed effects, and sample location as a random effect (*lmer* functions in the *lme4* package). For each season, brown trout and mottled sculpin stable isotope values were compared using Tukey-adjusted pairwise comparisons.

Isotopic niche breadth and overlap

Standard ellipse area (SEA) for brown trout and mottled sculpin in each sampling occasion was quantified to evaluate isotopic niche breadth (*groupMetricsML* functions in the *SIBER* package; Jackson & Parnell, 2023). SEA contains 40% of the data and represents the core isotopic niche of the population (Batschelet, 1981). Isotopic niche overlap (%) was then visually estimated by evaluating the overlap between brown trout and mottled sculpin SEAs for each sampling occasion.

2.4.4 | Statistical analyses and model assumptions

All descriptive and statistical analyses were performed in R 4.3.0 (R Core Team, 2023). Assumptions of normality and constant variance were assessed using residual diagnostic plots. Statistical significance was evaluated at $\alpha = .05$.

3 | RESULTS

3.1 | Prey availability (benthic macroinvertebrates)

There was a significant effect of season on BMI biomass ($F=3.5$, $p=.046$). Post-hoc Tukey-adjusted pairwise comparisons revealed BMI biomass was significantly higher in spring compared to autumn ($p=.04$), but there were no significant differences in BMI biomass between spring and summer ($p=.25$) or summer and autumn ($p=.44$). In 2021, mean BMI biomass was highest in spring (2777 mg/m^2), followed by summer (1865 mg/m^2) and autumn

(1221 mg/m²) (Figure S2). In 2022, mean BMI biomass was similarly higher in spring (3141 mg/m²) than in summer (2252 mg/m²) (Figure S2).

3.2 | Stomach content analysis

Nine percent of the 827 brown trout and 17% of the 758 mottled sculpin had empty stomachs, leaving 755 brown trout and 631 mottled sculpin stomach content samples for analysis (Table 1). The average number of prey items in the diets of mottled sculpin and juvenile brown trout exhibited seasonal (Poisson ANOVA: $p < .001$) and annual variation ($p < .001$). In spring, mottled sculpin diets contained an average of 4 prey items, which increased to 14 in summer and decreased to 3 in autumn. Brown trout diets averaged 20 prey items in spring, 37 in summer and 7 in autumn. Diet composition of brown trout and mottled sculpin varied seasonally (Figure 1). Based on dry weight estimates, Trichoptera contributed the most to brown trout diets in spring (44% in 2021 and 50% in 2022), summer (32%; 33%) and autumn (40%; 42%). Trichoptera contributed the most to mottled sculpin diets in spring of 2021 (42%) and 2022 (32%) and autumn of 2021 (29%). Ephemeroptera contributed the most to their diets in summer of 2021 (35%), and then Diptera in summer (34%) and autumn (29%) of 2022.

3.2.1 | Feeding intensity

There was a significant effect of season (brown trout: $p < .001$; mottled sculpin: $p < .001$), but not year (brown trout: $p = .27$; mottled sculpin: $p = .28$) on vacuity index (VI) for both species. VI did not significantly vary between spring and summer for brown trout ($p = .31$) or mottled sculpin ($p = .28$) but was significantly lower in autumn compared to spring and summer for both species ($p < .001$). Percent of empty stomachs ranged from 3% to 19% for brown trout and 7% to 34% for

mottled sculpin, with the highest proportion of empty stomachs occurring in autumn of both years for both species (Table 1). For brown trout, there was a significant effect of season ($p < .001$) and year ($p = .012$) on stomach fullness index (SFI). For mottled sculpin, there was a significant effect of season ($p < .001$) but not year ($p = .16$) on stomach fullness index. SFI did not significantly vary between spring and summer for brown trout ($p = .82$) or mottled sculpin ($p = .93$) but was significantly lower in autumn compared to spring and summer for both species ($p < .001$). Mean SFI ranged from 0.06% to 0.30% for brown trout and 0.09% to 0.40% for mottled sculpin, with the lowest SFI occurring in autumn of both years for both species (Table 1).

3.2.2 | Prey selectivity

Electivity index was generally close to 0 for major taxa (Trichoptera, Diptera, Ephemeroptera), showing that they were consumed in proportion to availability (Figure 2; Table S1). In 2021, juvenile brown trout positively selected for adult Coleoptera in spring ($E = 0.53$), adult Coleoptera ($E = 0.32$) and Trichoptera ($E = 0.67$) in summer and Ephemeroptera ($E = 0.37$) and Gastropoda ($E = 0.43$) in autumn. Mottled sculpin did not positively select for any prey in spring ($E < 0.3$) but selected for Amphipoda in summer ($E = 0.57$), and Diptera ($E = 0.49$) and Ephemeroptera ($E = 0.67$) in autumn. In 2022, juvenile brown trout positively selected for Amphipoda ($E = 0.36$) and Diptera ($E = 0.48$) in spring, and adult Coleoptera ($E = 0.52$) in summer. Mottled sculpin positively selected for Amphipoda ($E = 0.60$) and Oligochaeta ($E = 0.56$) in spring, and adult Coleoptera ($E = 0.35$) and Diptera ($E = 0.37$) in summer.

3.2.3 | Individual and population trophic niches

The total niche width (TNW), individual niche width (WIC), variation between individuals (BIC) and individual specialization (WIC/TNW)

Species	Year	Season	n	Length (mm)	Weight (g)	VI (%) ^a	SFI (%) ^a
Brown trout (80–200 mm)	2021	Spring	384	105 ± 27	15 ± 13	3	0.15 ± 0.24
		Summer	314	115 ± 20	19 ± 13	3	0.30 ± 0.43
		Autumn	366	106 ± 29	17 ± 15	19	0.06 ± 0.20
	2022	Spring	564	102 ± 26	14 ± 14	5	0.15 ± 0.16
		Summer	303	116 ± 22	20 ± 14	10	0.11 ± 0.23
		Autumn	193	106 ± 29	17 ± 15	17	0.10 ± 0.22
Mottled sculpin (80–135 mm)	2021	Spring	300	95 ± 8	14 ± 4	11	0.25 ± 0.38
		Summer	297	95 ± 9	13 ± 4	7	0.40 ± 1.15
		Autumn	287	93 ± 10	12 ± 4	34	0.10 ± 0.47
	2022	Spring	373	93 ± 10	12 ± 5	14	0.32 ± 0.76
		Summer	262	94 ± 10	12 ± 4	8	0.27 ± 0.49
		Autumn	232	95 ± 9	13 ± 4	23	0.09 ± 0.33

TABLE 1 Total number of individuals (n) within the study size range that were caught and processed. Mean ± SD length (mm) for brown trout (fork length; FL) and mottled sculpin (total length; TL), weight (g) and stomach fullness index (SFI). Vacuity index (VI) and SFI are in percentages (%).

^aDenotes sample sizes that differ from (n). VI and SFI were calculated using fish processed for SCA.

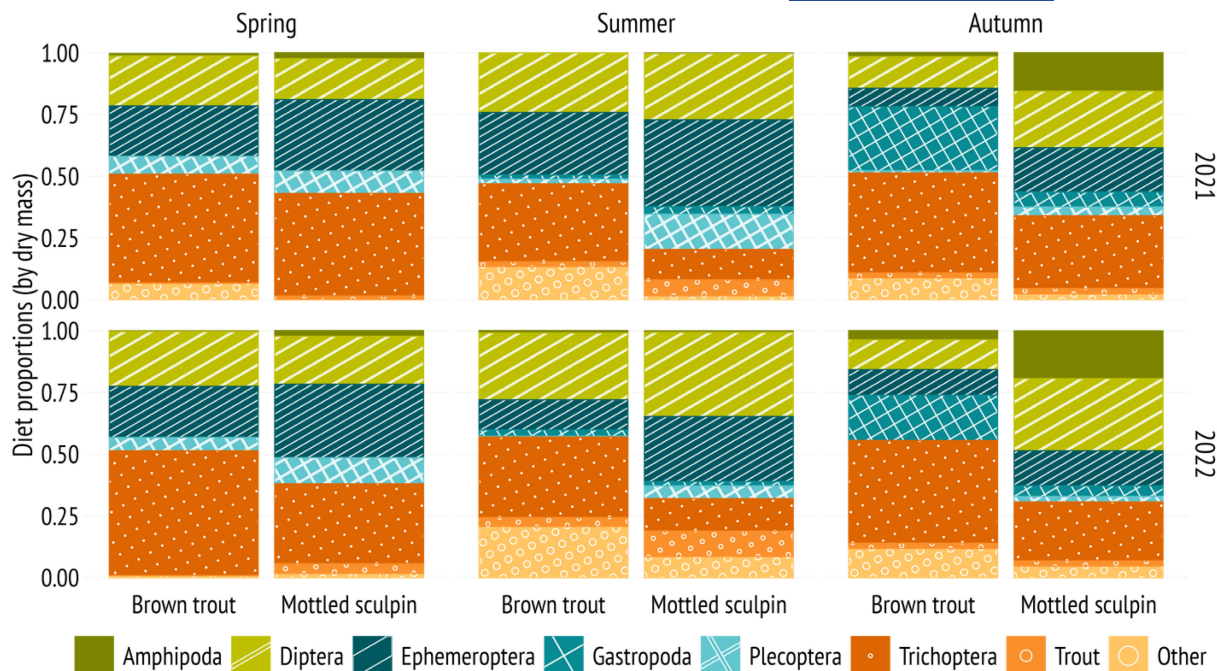


FIGURE 1 Mean proportion of prey groups (by dry mass) in diets of juvenile brown trout and mottled sculpin in spring (left), summer (middle) and autumn (right) of 2021 (top) and 2022 (bottom). Prey groups contributing less than 10% to the diet of either species in any season were grouped under 'Other' for improved clarity.

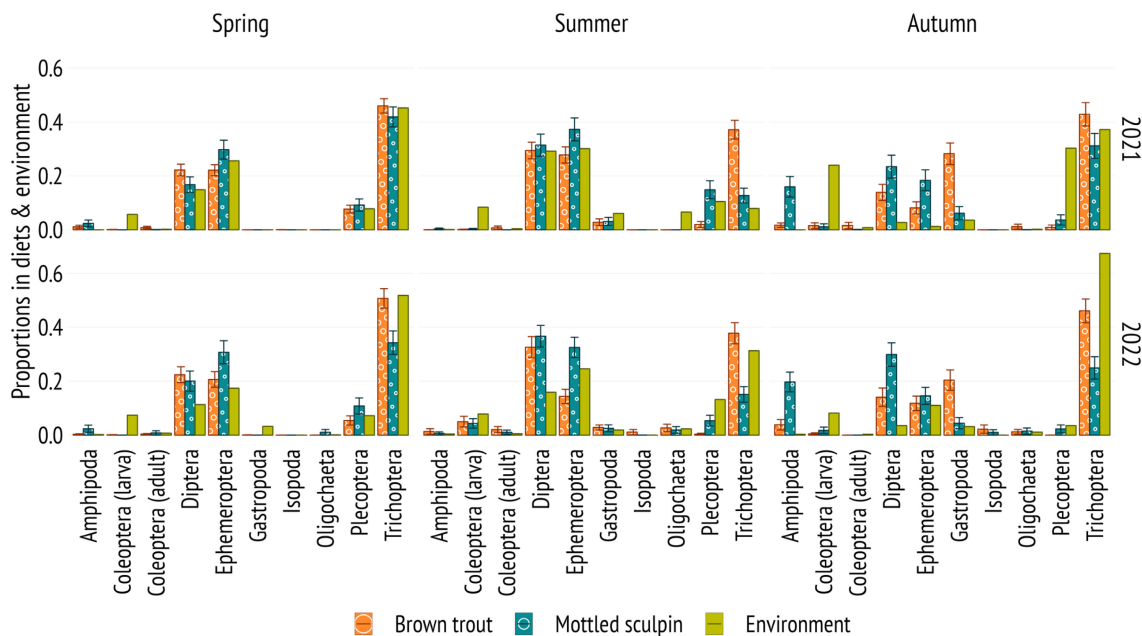


FIGURE 2 Mean \pm SE proportion of prey in the diets of mottled sculpin and juvenile brown trout, and in the environment (i.e. Surber samples), in spring (left), summer (middle) and autumn (right) of 2021 (top) and 2022 (bottom). Prey groups that were found in fish diets but not represented in the environment (or vice versa) were removed from analysis.

exhibited seasonal trends (Figure 3). Total niche width was narrowest in spring of 2021 and 2022 and widest in autumn of 2021 and in summer of 2022 for both brown trout and mottled sculpin. Individual niche width remained relatively consistent between spring and summer but in autumn of both years and for both species. On the other

hand, between-individual variation was lowest in spring, intermediate in summer and highest in autumn of 2022 for both brown trout and mottled sculpin. Additionally, individual specialization (WIC/TNW) was relatively high for both species across all sampling occasions (WIC/TNW < 0.5), and individuals showed the highest degree

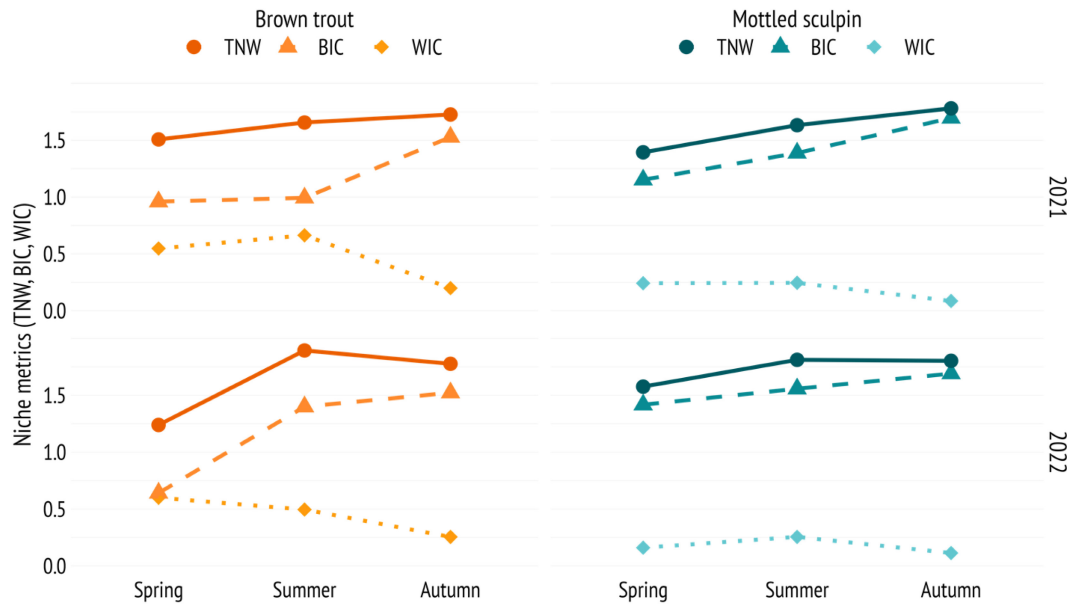


FIGURE 3 Seasonal variation in total niche width (TNW), between-individual component (BIC) and within-individual component (WIC) of juvenile brown trout (left) and mottled sculpin (right) in 2021 (top) and 2022 (bottom).

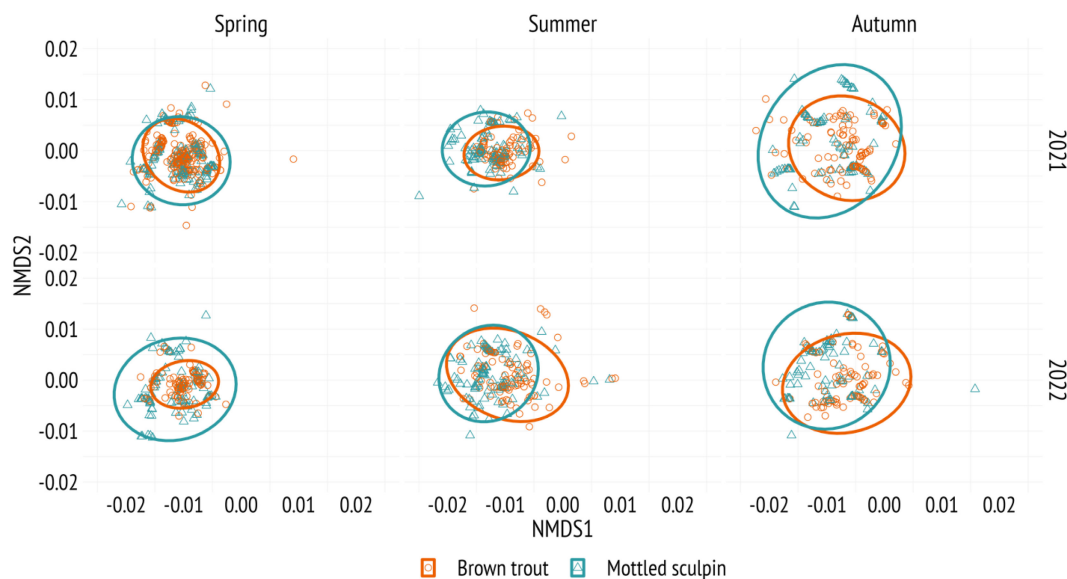


FIGURE 4 Non-metric multidimensional scaling (NMDS) of pairwise Bray-Curtis dissimilarities between brown trout (orange circles) and mottled sculpin (blue triangles) diets in spring (left), summer (centre) and autumn (right) in 2021 (top) and 2022 (bottom) (stress level=0.08). Ellipses represent 95% confidence intervals.

of specialization in autumn of both years, coinciding with resource limitation (Figure S2).

3.2.4 | Inter-specific trophic niche overlap

Trophic niche overlap between brown trout and mottled sculpin was high across all sampling occasions (Schoener's index >0.60), except for autumn of 2022 (0.59). The highest degree of overlap occurred in spring of 2021 (0.87) and 2022 (0.79), and the lowest occurred in autumn of both years (0.62 in 2021 and 0.59 in 2022) (Figure S3).

3.2.5 | Diet composition

The PERMANOVA analysis found species (pseudo- $F=24.9$, $p<.001$), season (pseudo- $F=44.36$, $p<.001$) and year (pseudo- $F=2.3$, $p=.044$) contributed to variation in diet composition, and the effect of species varied by season (species*season; pseudo- $F=11.55$, $p<.001$) (Table S2). Pairwise PERMANOVA comparisons found significant differences in diet composition between brown trout and mottled sculpin in all seasons in 2021 and 2022 ($p<.05$), except for spring of 2021 ($p=.13$). There were no significant differences in group dispersion between brown trout and mottled sculpin in summer 2021 ($p=.13$),

summer 2022 ($p=.99$) or in autumn 2022 ($p=.86$), indicating that the extent of intra-specific diet variation was similar between the species. However, there were significant differences in group dispersion in spring 2022 ($p<.001$) and autumn 2021 ($p=.003$). Subsequent evaluation of NMDS plots indicated that the differences between species in autumn 2021 and spring 2022 could be attributed to both the variation in dispersion and diet composition (Figure 4).

The SIMPER analysis results revealed that prey groups contributing to diet differences between brown trout and mottled sculpin varied across sampling occasions. In spring of 2022, Trichoptera (relative contribution=20%, $p=.02$) and Plecoptera (7%, $p=.01$) significantly contributed to differences in diet composition. In summer of 2021, differences in diet were due to terrestrial insects (5%, $p<.001$) and emergent aquatic insects (3%, $p=.046$), while in summer of 2022 trout (6%, $p=.001$), terrestrial insects (5%, $p<.001$), larval Coleoptera (4%, $p<.001$), adult Coleoptera (1%, $p=.01$) and Oligochaeta (2%, $p<.001$) all contributed to differences. In autumn of 2021, Trichoptera (24%, $p<.001$), Gastropoda (15%, $p<.001$), Amphipoda (7%, $p<.001$) and the rare prey group (1%, $p=.003$) contributed to differences. In autumn of 2022, Trichoptera (22%, $p<.001$), Gastropoda (11%, $p<.001$), Amphipoda (9%, $p<.001$) also contributed to diet differences, as well as Isopoda (1%, $p<.001$).

3.3 | Stable isotope analysis

A total of 955 fish (brown trout=513, mottled sculpin=442) were sampled for stable isotope analysis. There was a significant effect of species ($F=34.25$, $p<.001$) and season ($F=34.25$, $p<.001$) on $\delta^{15}\text{N}$ isotope values, and the effect of species varied by season

(species * season; $F=30.29$, $p<.001$). There was no significant effect of year on $\delta^{15}\text{N}$ values ($p=.84$). Brown trout were more depleted in $\delta^{15}\text{N}$ compared to mottled sculpin in spring ($p=.01$) and autumn ($p<.001$), although differences in mean $\delta^{15}\text{N}$ values were relatively small, ranging from 0.01‰ to 1.11‰. No significant difference in mean $\delta^{15}\text{N}$ was found between the two species in summer ($p=.08$). There was evidence of a significant effect of species ($F=39.53$, $p<.001$), season ($F=206.52$, $p<.001$) and year ($F=496.94$, $p<.001$) on $\delta^{13}\text{C}$ isotope values, and the effect of species varied by season (species*season; $F=3.85$, $p=.02$). Brown trout were more enriched in $\delta^{13}\text{C}$ compared to mottled sculpin in summer ($p<.001$) and autumn ($p<.001$), but no significant difference in mean $\delta^{13}\text{C}$ was found between the two species in spring ($p=.15$).

The estimated isotopic niche width (standard ellipse area) varied across species, seasons and years (Figure 5). In 2021, mottled sculpin displayed a broader isotopic niche compared to brown trout throughout all seasons. Additionally, SEA increased from spring to autumn for both brown trout (spring=1.5; summer=1.6; autumn=1.8) and mottled sculpin (spring=1.8; summer=2.3; autumn=2.5) in 2021. However, in 2022, brown trout SEA was narrowest in spring (SEA=1.5) and widest in summer (SEA=2.5) and for mottled sculpin SEA was narrowest in autumn (SEA=1.6) and widest in spring (SEA=2.7). Isotopic niche overlap varied seasonally (Figure 5). In 2021, the highest percent overlap occurred in summer and the lowest in autumn. While in 2022, the highest percent overlap occurred in spring and the lowest in summer. In both years, the isotopic niche widths were more seasonally dynamic in brown trout compared to mottled sculpin (Figure 5), suggesting that brown trout consumed prey items more flexibly based on their availability.

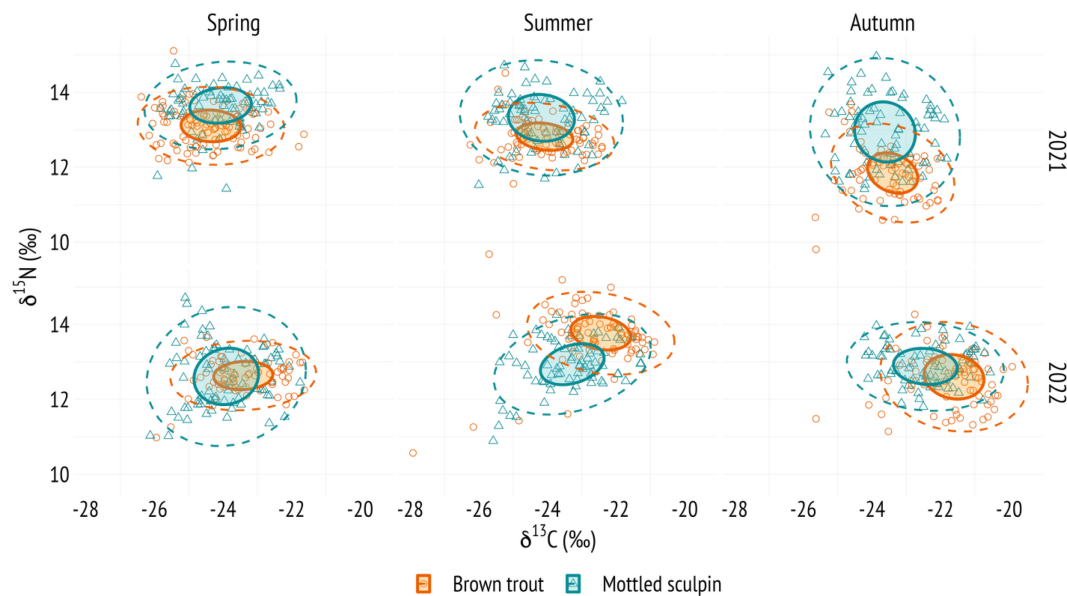


FIGURE 5 Seasonal variation in isotopic niches of juvenile brown trout (orange circles) and mottled sculpin (blue triangles) in spring (left), summer (middle) and autumn (right) in 2021 (top) and 2022 (bottom). Dashed ellipses represent stable isotope ellipse areas using 95% of the data, while solid ellipses represent Standard Ellipse Areas (SEA) using 40% of the data.

4 | DISCUSSION

As predicted, both mottled sculpin and juvenile brown trout shifted their trophic niches in response to seasonal changes in resource availability. Benthic macroinvertebrate (BMI) biomass peaked in spring and declined through summer and autumn, which is consistent with seasonal BMI patterns in other unregulated rivers (Kato et al., 2003; Rundio & Lindley, 2008). Both mottled sculpin and juvenile brown trout, for the most part consumed prey items relative to their proportional availability, thus resource availability fundamentally defined feeding opportunities. When resources became scarce in autumn, both species consumed less, as evidenced by the fewer prey items in their diets, higher proportion of empty stomachs and lower stomach fullness. In this time of resource scarcity, individuals diverged in resource use and developed more specialized diet patterns, which resulted in population-level trophic niche expansion in both species. These findings support our initial predictions that resource limitation would promote population-level trophic niche expansion via increased diet variation among individuals.

The patterns in resource use are consistent with previous findings from both regulated and unregulated systems, which have demonstrated that intra-specific competition promotes individual specialization and niche variation within populations (Evangelista et al., 2014; Latli et al., 2019). In both species, individuals compete with conspecifics for food resources and the intra-specific competition is most conspicuous among individuals of similar body size (Hin & de Roos, 2019). We sampled individuals of similar body size in mottled sculpin (80–135 mm TL) and brown trout (80–200 mm, but 80% were 80–150 mm), and found that fish catch-per-unit-effort was relatively consistent for both species across seasons (brown trout: 0.02–0.07 fish/m²; mottled sculpin: 0.02–0.04 fish/m²). This suggests that intra-specific competition likely contributed to the observed patterns of individual specialization and niche partitioning. In addition, the thermal regime of our regulated study river has been altered due to upstream dams releasing hypolimnetic water, such that water temperature remains relatively cool during spring and summer but becomes warmer in autumn and winter compared to an unregulated reference stream (Figure S1). Peak monthly average stream temperatures occurred in October 2021 (10.8°C) and September 2022 (11.9°C), falling slightly below approximated optimal growth ranges for mottled sculpin (12–16°C; Kanno et al., 2023) and brown trout (12–18°C; Bell, 2006). These data suggest that while warmer autumn temperatures facilitated favourable conditions for fish growth, limited food resources and reduced feeding activity (indicated by higher VI and lower SFI) during this period likely intensified intra-specific competition, ultimately leading to individual specialization and trophic niche partitioning within each species. Finally, we acknowledge the potential for inflated metrics of individual specialization due to consumption of very few food items (1–2 items) (Zaccarelli et al., 2022). However, this concern is likely mitigated in our study, as brown trout consumed a considerable amount of prey across all seasons (mean: ≥5), and mottled sculpin

consumed similarly small numbers of prey in spring and autumn in 2021 (mean: 4 in spring; mean: 2 in autumn) and 2022 (mean: 3 in spring and autumn). Accordingly, observed patterns of individual specialization and trophic niche partitioning should not be attributed to sampling artefacts, particularly given that stable isotopes support these results. Our SIA results revealed population-level isotopic niche expansion in autumn compared to spring (both species in 2021 and brown trout in 2022), which was driven by greater dispersion between individuals in the population.

Our SCA results also revealed significant trophic niche overlap between mottled sculpin and juvenile brown trout across all seasons, indicating these two species use similar resources, a pattern commonly observed between juvenile salmonids and cottids in unregulated rivers (Gabler & Amundsen, 1999; Hesthagen et al., 2004). However, the extent of overlap varied seasonally and did not align with our initial prediction. We expected inter-specific trophic niche overlap to increase during periods of resource scarcity, as a result of both populations expanding their trophic niches and relying on similar prey. Contrary to our prediction, overlap peaked in spring, when resources were most abundant, and gradually declined through summer and autumn as resources became more limited. In spring and summer, both species mainly relied on Ephemeroptera, Trichoptera and Diptera, however in autumn, brown trout incorporated Gastropoda into their diet, while mottled sculpin consumed more Amphipoda. This dietary shift indicates that mottled sculpin and juvenile brown trout partitioned resources to some extent when resources were limited in autumn. This finding aligns with previous research that has observed temporal variation in resource use and trophic niche partitioning among other salmonid and cottid species (Abedi et al., 2023; Falke et al., 2020; Marcarelli et al., 2020). Such flexibility in trophic niche partitioning is considered an important mechanism to minimize competition and facilitate the coexistence of sympatric species especially when resources are limited (Chesson, 2000; Pianka, 1974; Schoener, 1974). In essence, the abundance of resources in spring likely reduces the pressure for niche segregation between mottled sculpin and juvenile brown trout (Langeland et al., 1991; Nilsson, 1963), whereas resource limitation in autumn potentially drives trophic niche partitioning between the two species, minimizing competition and facilitating their coexistence.

Interestingly, the observed reduced trophic niche overlap between mottled sculpin and juvenile brown trout in autumn corresponded to population-level trophic niche expansion via increased diet variation among individuals. This result indicates that trophic niche partitioning occurred both within and between species. Several studies have observed decreased trophic niche overlap between species despite populations expanding their trophic niche breadth (Costa-Pereira et al., 2019; Liu et al., 2019; Prati et al., 2021). However, few studies, to our knowledge, have identified trophic niche expansion as a consequence of niche differentiation among individuals within the population, alongside a reduction in trophic niche overlap between species (Thomas et al., 2017). Our SCA findings demonstrate that inter- and intra-specific trophic niche

partitioning can occur simultaneously, potentially reducing competition both within and between species.

Similar to our SCA findings, SIA revealed seasonal variation in isotopic niche breadth and overlap between mottled sculpin and juvenile brown trout. Isotopic niches were broader in autumn and narrower in spring for both species in 2021, and for juvenile brown trout in 2022. The degree of isotopic niche overlap was greater in spring compared to autumn in both years. These results support our SCA findings, which indicated that both species exhibited narrower trophic niches and shared more resources in spring, while in autumn, mottled sculpin and juvenile brown trout diverged in resource use and consumed a wider range of resources. In addition, stable isotopic analysis showed that brown trout were characterized with more seasonally dynamic isotopic niche widths and flexible diet selections than mottled sculpin, a unique insight gained in SIA but not SCA. This finding shows that brown trout and mottled sculpin do not respond identically to seasonal resource fluctuations, which could be driven by differences in their foraging ecology. Brown trout are generalist foragers, but sculpin are benthivorous fish, which may limit them to fewer prey types and restrict their trophic niche flexibility. Additionally, the observed variation in seasonal isotopic niches could be due to asymmetrical competition between the two species (Hesthagen & Heggenes, 2003; Zimmerman & Vondracek, 2007). However, it is important to note some discrepancies between the SCA and SIA results. Specifically, mottled sculpin's isotopic niche breadth contracted from spring to autumn in 2022, which does not align with our SCA findings. Additionally, isotopic niche overlap was highest in summer in 2021 and lowest in the summer of 2022, despite clear SCA trends indicating a gradual decline in trophic niche overlap from spring to autumn in both years.

Previous studies have observed inconsistencies between SIA and SCA results due to turnover time of stable isotopes in the tissues (Burbank et al., 2019; Futia et al., 2021). As stable isotopes reflect what has been assimilated into an organism's tissue, it could represent consumption several weeks to months before sampling (Nielsen et al., 2018), whereas SCA provides a 'snapshot' of diet composition at the time of sampling. Furthermore, turnover time varies with growth and metabolic rates (Matley et al., 2016). Higher metabolic rates, often associated with warmer temperatures (Volkoff & Rønnestad, 2020) or specific developmental stages (Sibly et al., 2015), increase turnover rates and thus may reflect what the organism consumed more recently compared to samples taken during periods of slower growth or metabolic rates (Matley et al., 2016; Vander Zanden et al., 2015). In our study system, stream temperatures peak from July to October, which corresponds to our summer and autumn sampling periods. Therefore, the observed SIA trends do not necessarily reflect expected discrepancies from differences in turnover rates. It is difficult to determine whether the differences in SIA and SCA results are due to the 'lag' of tissue turnover or if stable isotopes more accurately represent the variety of prey brown trout and mottled sculpin were consuming in summer. Despite these discrepancies,

SIA results corroborate the key findings of SCA, of reduced overlap in autumn compared to spring.

In conclusion, this study demonstrates the importance of evaluating trophic dynamics at both the individual- and population-level to understand seasonal trophic niche overlap among sympatric species. The seasonal fluctuations in trophic niche dynamics emphasize the need for conducting research with temporal replicates, particularly in the context of regulated rivers, where altered flows may disrupt seasonal resource availability compared to natural systems. These variations in resource availability across seasons and between rivers may be a key factor contributing to differences in intra- and inter-specific trophic niche dynamics reported among previous studies (Bloomfield et al., 2022; Costa-Pereira et al., 2017). Our findings indicate that when faced with resource limitation, juvenile brown trout and mottled sculpin individuals developed more specialized diet patterns to reduce competition. This may be a potential mechanism that prevents competitive exclusion and instead facilitates the coexistence of sympatric fish species not only in this stream with a highly altered flow regime, but also in other less disturbed streams (Liu et al., 2019; Nakano et al., 1999; Neves, Costa-Pereira, et al., 2021; Neves, Kratina, et al., 2021). However, such a mechanism might not persist if environmental stressors such as climate change or other anthropogenic disturbances intensify resource limitation or prolong its duration (e.g. droughts; Lennox et al., 2019). Further research is warranted to synthesize the context-dependency of trophic niche dynamics among sympatric fish species in regulated and unregulated rivers.

AUTHOR CONTRIBUTIONS

YK, BMJ and BPR conceived and designed the study. NMP performed laboratory and statistical analysis and drafted the manuscript. All authors conducted fieldwork and contributed to the writing of this manuscript.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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