THESIS

SEASONAL TROPHIC NICHE DYNAMICS OF MOTTLED SCULPIN AND JUVENILE BROWN TROUT IN A REGULATED ROCKY MOUNTAIN RIVER

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ABSTRACT

SEASONAL TROPHIC NICHE DYNAMICS OF MOTTLED SCULPIN AND JUVENILE BROWN TROUT IN A REGULATED ROCKY MOUNTAIN RIVER

In temperate ecosystems, resource availability fluctuates seasonally due to changes in environmental conditions and productivity throughout the year. 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 highly variable among regions and communities. In this study, we analyzed stomach content samples and stable isotope signatures to evaluate seasonal trophic niche dynamics of mottled sculpin Cottus bairdii (80-130 mm total length) and juvenile brown trout Salmo trutta (80-200 mm) in the Blue River, Colorado, USA, where aquatic production varies seasonally and has been reduced due to upstream dams. Prey biomass (i.e., benthic macroinvertebrates) peaked in spring and declined through summer and autumn. Stomach content and stable isotope analysis results revealed diet composition of mottled sculpin and brown trout shifted seasonally in response to changes in resource availability. 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. Interspecific trophic niche overlap was relatively high across all seasons, but the lowest degree of overlap occurred in autumn of both years. Isotopic analysis revealed similar trends of wider isotopic niches and reduced overlap in autumn compared to spring. Taken together, our data indicate that seasonal variation impacts individual and population-level trophic niche dynamics, as well as interspecific niche overlap between mottled sculpin and juvenile brown trout. These two species occur sympatrically in many

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coldwater streams throughout North America, and our findings indicate trophic segregation under resource limitation may serve as a mechanism that facilitates their coexistence.

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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; Fry et al., 1999; Jirka & Kraft, 2017) and the degree of intraspecific 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 is often attributed to cause extirpations of a less competitive species (Bøhn et al., 2008; Levine & HilleRisLambers, 2009; Macarthur & Levins, 1967; Schoener, 1974; Wei et al., 2021). 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 (Costa-Pereira et al., 2017; Falke et al., 2020; Neves et al., 2021; Silva et al., 2014). Quantifying this temporal pattern is becoming more important in the contemporary context of stream fish management because anthropogenic disturbances such as dams and climate change are shifting seasonality and phenology in lotic ecosystems (Bloomfield et al., 2022; Khelifa et al., 2021; Poff et al., 1997; Staudinger et al., 2021; Wang et al., 2016).

Trophic niche width reflects the range of resources an individual or population utilizes (Roughgarden, 1972) and can expand or contract in response to resource availability and the relative intensity of intra- and interspecific 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 interspecific competition is expected to result in 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 interspecific competition have been observed across various studies (Bolnick et al., 2010; Costa-Pereira et al., 2017, 2019; Hammerschlag et al., 2010; Sánchez-Hernández et al., 2021). Similarly, sympatric species are expected to diverge in resource use, often through niche contraction, to minimize niche overlap and interspecific competition (Britton et al., 2018; Frossard et al., 2021; Larocque et al., 2021; Levine & HilleRisLambers, 2009; Neves et al., 2021; Prati et al., 2021; Tran et al., 2015).

Conversely, increased intraspecific competition has consistently been associated with increased individual specialization and population niche expansion (Araújo et al., 2008; Cachera et al., 2017; Evangelista et al., 2014; Latli et al., 2019; Svanbäck & Bolnick, 2007; Svanbäck & Persson, 2004). In this context, niche expansion results from greater trophic niche partitioning among individuals within the population (between-individual variation), while individual niches can remain constant or 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 (Bloomfield et al., 2022; Costa-Pereira et al., 2017; Cutting et al., 2016; Silva et al., 2014).

Salmonids and cottids are two widely distributed groups of fish that co-occur in many rivers and lakes in the northern hemisphere (Becker, 1983). While sculpin are often considered

potential prey for trout (Brandt, 1986; Meredith et al., 2015), juvenile trout and sculpin share similar dietary preferences, primarily consuming benthic macroinvertebrates and other small prey items (Adams & James, 2008; Becker, 1983). Previous studies have found that various salmonid and cottid species occupy similar niches and may compete for habitat or prey, but these results have been inconsistent (Gabler & Amundsen, 1999; Hesthagen et al., 2004; Holmen et al., 2003; Hudson et al., 1995; Larocque et al., 2021; Louhi et al., 2014). Additionally, limited studies have examined how trophic niche dynamics among these groups of fishes may vary temporally, even though seasonal variation in resource availability is typical in temperate systems where cottids and salmonids co-exist (Bogan & Lytle, 2007; Kato et al., 2003; Rundio & Lindley, 2008). Mottled sculpin (Cottus bairdii), a small-bodied native fish, and brown trout (Salmo trutta), a non-native fish, coexist in many coldwater streams throughout North America (Becker, 1983). Despite their prevalence, few studies have evaluated the trophic dynamics between these two specific species (Larocque et al., 2021). Evaluating these trophic dynamics could provide valuable insights into population and community dynamics of mottled sculpin and juvenile brown trout, as well as other salmonids and cottids that are widely distributed and co-exist in temperate streams throughout the northern hemisphere.

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, and offers a more time-integrated representation of an organism's niche (Matley et al., 2016; Post, 2002). 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. Our specific objectives were to evaluate variation in: (1) feeding intensity; (2) diet composition; (3) individual and population trophic niche breadth; and (4) interspecific trophic niche overlap, in relation to seasonal shifts in resource availability.

2 | MATERIALS & 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 (3,900 m elevation) and has a watershed area of 1,800 km². This region experiences a temperate climate with seasonal variation in temperature (annual mean: 4.6°C) and precipitation (annual mean: 517mm). There are two large, hypolimnetic release reservoirs on the Blue River upstream of the study area: Dillon Reservoir (317,379,811 m³) and Green Mountain Reservoir (190,751,799 m³). These reservoirs serve multiple purposes including supplying municipal and irrigation water to local communities, generating hydroelectric power, and diverting water to the eastern slope of the Rockies. The reservoirs have reduced nutrient availability downstream of the impoundments, as well as altered thermal and flow regimes (Figure S1). In this context, the Lower Blue River experiences temporal variation in resource availability.

2.2 | Field sampling

Sampling was conducted at five sites, each approximately 100 meters in length, along a 4 km stretch of the Lower Blue River. Sampling took place at each site in spring, summer, and autumn of 2021 and 2022. 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). If the target number of fish for sample collection was not obtained during the initial three passes, additional sampling was performed. All fish 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 brown trout (80 - 200 mm) and 30 mottled sculpin (80 - 140 mm) were anesthetized (AQUI-S®, Lower Hutt, New Zealand) and gastric lavaged to obtain stomach

content samples. Of these fish, 15 individuals of each species, ranging in size, were sacrificed for analysis of stable isotopes and energy density estimates. Stomach content samples and sacrificed fish were placed on ice while in the field and subsequently frozen at the laboratory, until they were processed. In addition to fish sampling, benthic macroinvertebrates were sampled within 1-2 weeks of our fish sampling (except for autumn of 2022). At each sample site, three random samples were collected from both the top and bottom of the reach using a Surber sampler (1 ft²). These samples were pooled (one for top reach and one for bottom reach) and subsequently sent to the Aquatic Biology Associates for identification, and abundance and biomass estimates.

2.3 | Laboratory sample preparation & 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 fourteen 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 then characterized as the proportional dry mass of prey groups present in relation to total stomach content dry mass:

$$W_i = \frac{W_i}{\sum_{i=1}^Q W_i}$$

where W_i is the weight of prey type i, and Q is the number of prey groups in an individual's stomach.

2.3.2 | Stable isotope analysis

Sacrificed fish were dried at 60°C for a minimum of 72 hours or until dry weight stabilized. The dry weights of whole fish were used for energy density estimates (see details below). Additionally, a skinless and boneless dorsal muscle tissue sample was collected from each fish for stable isotope analysis. Muscle tissue samples were ground into a homogenized powder and sent to The Cornell Isotope Laboratory, where a Thermo Delta V ratio mass spectrometer connected to an NC2500 elemental analyzer was used to measure elemental percentage of *N* (%N) and *C* (%C), and the corrected isotope delta value for 15N ($\delta^{15}N$) and 13C ($\delta^{13}C$) (Fry, 2006). $\delta^{15}N$ and $\delta^{13}C$ were measured in parts per mil (‰) and calculated as:

$$\delta_{isotope} = \left[\left(\frac{R_{sample}}{R_{standard}} - 1 \right) \right] * 1000$$

where *R* is the ratio of heavy to light carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotopes in the samples and a reference standard sample (atmospheric air for $\delta^{15}N$, and Vienna Pee Dee Belemnite for $\delta^{13}C$) (Fry, 2006). Data were not lipid normalized because the mean C:N ratio was 3.25 for brown trout and 3.36 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-adjusted pairwise comparisons. Sites were pooled because we found no significant effect of site on BMI biomass (F = 0.34, p = 0.85).

2.4.2 | Fish condition

Condition factor and energy density were calculated to evaluate seasonal variation in fish condition. The condition factor (K) was estimated for each fish processed in the field, and was calculated as (Froese, 2006; Fulton, 1911):

$$K = \frac{W}{L^3} * 100$$

Where W is the wet weight of the fish (g) and L is the length of the fish (cm: FL for brown trout and TL for mottled sculpin). Energy density (ED) was estimated for each fish that had been sacrificed and dried in the laboratory, and was calculated as (Johnson et al., 2017):

$$ED = 32.678 \times DM^{1.604}$$

Where *DM* is relative dry matter content and is calculated as:

$$DM(\%) = 100 \left(\frac{dry mass(g)}{wet mass(g)} \right)$$

Linear mixed models were fit using condition factor and energy density as the response variables. The models included season and year as fixed effects, and sample site as a random effect. Seasonal differences in condition factor and energy density for brown trout and mottled sculpin were compared using Tukey-adjusted pairwise comparisons.

2.4.3 | Stomach content analysis

2.4.3.1 | 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 and is calculated as (Hureau, 1970):

$$VI = \frac{S_E}{S_T} \times 100$$

Where S_E is the number of empty stomachs and S_T is the total number of stomachs analyzed. Stomach fullness index (SFI) is a measure of how much food an individual has eaten relative to their weight and is calculated as:

$$SFI = \frac{S_W}{F_W - S_W} \times 100$$

where S_W is the estimated dry mass of diet contents in an individual's stomach (mg) and F_W is the wet weight of the fish (mg). 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.

2.4.3.2 | Prey selectivity

To evaluate prey selectivity of mottled sculpin and juvenile brown trout across seasons, we used the electivity index (Vanderploeg & Scavia, 1979b, 1979a), which is based on Chesson's index (J. Chesson, 1978, 1983). Chesson's index is calculated as:

$$T_i = \frac{\left(\frac{d_i}{e_i}\right)}{\Sigma\left(\frac{d_i}{e_i}\right)}$$

Where d_i is the mean proportion of prey type i in the population's diet and e_i is the proportion of prey type i in the environment. Prey availability in the environment was based on the BMI biomass data. Prey groups found in fish diets but not represented in BMI community data (or vice versa) were excluded from the analysis. Electivity index was then calculated as:

$$E_i = \frac{(T_i - \frac{1}{n})}{(T_i + \frac{1}{n})}$$

Where n is the number of different prey types in the environment. Electivity values range from -1 to 1, where 0 indicates prey are being consumed in proportion to their availability in the environment, -1 indicates avoidance, and +1 indicates positive selection.

2.4.3.3 | Individual & population trophic niches

To evaluate seasonal variation in resource use, we estimated 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), which is a measure of the average niche width of individuals within a population, and 2) between individual component (BIC), which is a measure of the variation in niche positions between individuals (Roughgarden, 1972). The ratio of WIC to TNW (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 specialized diets, while larger WIC/TNW values suggest individuals with more generalist diets. TNW, WIC, BIC and WIC/TNW were based on dry mass values of the prey groups and calculated using the WTdMC function in the *RInSp* package (Zaccarelli et al., 2022), which uses the following equations (Bolnick et al., 2002; Roughgarden, 1972):

$$WIC = \sum_{i} p_{i}(-\sum_{k} p_{ik}ln(p_{ik}))$$

$$BIC = \sum_{k} p_{i}ln(p_{i}) - \sum_{k} q_{k}(-\sum_{i} t_{ik}ln(t_{ik}))$$

$$TNW = -\sum_{k} q_{k} ln(q_{k})$$

Where p_i is the proportion of the population's total use of resources that was used by individual *i*, p_{ik} is the proportion of resource category *k* in the diet of individual *i*, t_{ik} is the proportion of the population's total use of resource *k* that was used by individual *i*, and q_k is the average proportion of resource category *k* in the population's niche. The average proportion approach refers to calculating prey proportions in individual diets and then averaging those proportions across all individuals within the population. We chose this approach over the "sum" method 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. Additionally, we excluded statistical tests generated by the WTdMC function. The Monte Carlo resampling procedure is only applicable to prey count data, but not dry mass data (Zaccarelli et al., 2022).

2.4.3.4 | Inter-specific trophic niche overlap

Seasonal trophic niche overlap between brown trout and mottled sculpin was estimated using Schoener's index of overlap (Schoener, 1970):

$$D = 100 \left(1 - \frac{1}{2} \sum_{i} |p_{ai} - p_{bi}| \right)$$

where p_{ai} and p_{bi} are the average proportions of prey *i* in the diets of species *a* and *b*, respectively. 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).

2.4.3.5 | Diet composition

Differences in diet composition between groups were tested using a permutational multivariate analysis of variance (PERMANOVA; *adonis2* function in the *vegan* package; Oksanen et al., 2015). 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 9,999 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). 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 9,999 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.

2.4.4 | Stable isotope analysis

2.4.4.1 | Isotopic composition

Differences in mean $\delta^{15}N$ and $\delta^{13}C$ 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 (*Imer* functions in the *Ime4* package). For each season, brown trout and mottled sculpin stable isotope values were compared using Tukey-adjusted pairwise comparisons.

2.4.4.2 | Isotopic niche breadth & overlap

Standard ellipse area (SEA) for brown trout and mottled sculpin in each season and year were 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 estimated by calculating the overlap between brown trout and mottled sculpin SEA (as a percentage of the two ellipses that overlap with each other) for each sampling occasion (*maxLikOverlap* function in the *SIBER* package).

2.4.5 | Statistical analyses & 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 $\alpha = 0.05$.

3 | RESULTS

3.1 | Prey availability (benthic macroinvertebrates)

Benthic macroinvertebrate biomass differed significantly between seasons (F = 3.5, p = 0.046). Post-hoc Tukey-adjusted pairwise comparisons revealed significant differences in biomass between spring and autumn (p = 0.04), but there was no evidence of significant differences in BMI biomass between spring and summer (p = 0.25) or summer and autumn (p = 0.44). In 2021, mean BMI biomass was highest in spring (2777 mg/m²), followed by summer (1865 mg/m²) and autumn (1221 mg/m²) (Figure S2). In 2022, mean BMI biomass was highest in spring (3141 mg/m²) and followed by summer (2252 mg/m²) (Figure S2).

3.2 | Fish condition

There was a significant effect of season (brown trout: $\chi^2 = 128.64$, p < 0.001; mottled sculpin: $\chi^2 = 43.26$, p < 0.001), but not year (brown trout: $\chi^2 = 2.49$, p = 0.11; mottled sculpin: $\chi^2 = 0.33$, p = 0.57) on condition factor (K) for both species. K significantly varied between spring and summer for brown trout (p < 0.001) and mottled sculpin (p < 0.001), as well as spring and autumn for both species (p < 0.001). K did not vary significantly between summer and autumn for brown trout (p = 0.09) or mottled sculpin (p = 0.24). For brown trout, there was a significant effect of season ($\chi^2 = 44.31$, p < 0.001), but not year ($\chi^2 = 0.04$, p = 0.84) on energy density (ED). ED significantly varied between spring and summer (p < 0.001) and spring and autumn (p < 0.001), but not between summer and autumn (p = 0.85). For mottled sculpin, there was not a significant effect of season ($\chi^2 = 4.16$, p = 0.13) or year ($\chi^2 = 0.09$, p = 0.76) on ED. For brown trout in 2021, K and ED were highest in summer and lowest in spring (Table 1). In 2022, the highest K and ED occurred in autumn, and lowest in spring. For mottled sculpin in 2021, K and ED were highest in spring.

spring and lowest in autumn. In 2022, K and ED were highest in autumn, and lowest in summer, but spring for ED.

3.3 | 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 variation. 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.

3.3.1 | Feeding intensity

There was a significant effect of season (brown trout: $\chi^2 = 33.44$, p < 0.001; mottled sculpin: $\chi^2 = 40.05$, p < 0.001), but not year (brown trout: $\chi^2 = 1.23$, p = 0.27; mottled sculpin: $\chi^2 = 1.15$, p = 0.28) on vacuity index (VI) for both species. VI did not significantly vary between spring and summer for brown trout (p = 0.31) or mottled sculpin (p = 0.28) but was significantly lower in autumn compared to spring and summer for both species (p < 0.001). 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; Figure S3). For brown trout, there was a significant effect of season (χ^2 = 84.36, p < 0.001) and year (χ^2 = 6.31, p = 0.012) on stomach fullness index (SFI). For mottled sculpin, there was a significant effect of season (χ^2 = 104.97, p < 0.001) but not year (χ^2 = 1.98, p = 0.16) on stomach fullness index. SFI did not significantly vary between spring and summer for brown trout (p = 0.82) or mottled sculpin (p = 0.93) but was significantly lower in autumn compared to spring and summer for both species (p < 0.001) (Table 1; Figure S4).

3.3.2 | Prey selectivity

Electivity index was generally close to 0 for major taxa (Trichoptera, Diptera, Ephemeroptera) with some high values during specific seasons (Figure 2; Figure 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. While mottled sculpin did not positively select for any prey in spring (E < 0.3), 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.

3.3.3 | Individual & population trophic niches

The total niche width (TNW), individual niche width (WIC), variation between individuals (BIC), and individual specialization (WIC/TNW) 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 declined 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 of specialization in autumn of both years.

3.3.4 | Inter-specific trophic niche overlap

Trophic niche overlap between brown trout and mottled sculpin was high across all sampling occasions (H > 0.60), except for autumn of 2022 (H = 0.59). The highest degree of overlap occurred in spring of 2021 (H = 0.87) and 2022 (H = 0.79), and the lowest occurred in autumn of both years (2021: H = 0.62; 2022: H = 0. 59) (Figure S3).

3.3.5 | Diet composition

The PERMANOVA analysis found species (pseudo-F = 24.9, p < 0.001), season (pseudo-F = 44.36, p < 0.001) and year (pseudo-F = 2.3, p = 0.044) contributed to variation in diet composition, and the effect of species varied by season (species*season; pseudo-F = 11.55, p < 0.001) (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 < 0.05), except for spring of 2021 (p = 0.13). There were no significant differences in group dispersion between brown trout and mottled sculpin in summer 2021 (p = 0.13), summer 2022 (p = 0.99) or in autumn 2022 (p = 0.86). However, there were significant differences in group dispersion in spring 2022 (p < 0.001) and autumn 2021 (p = 0.03). 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 = 0.02) and Plecoptera (7%, p = 0.01) significantly contributed to differences in diet composition. In summer of 2021, differences in diet were due to terrestrial insects (5%, p < 0.001) and emergent aquatic insects (3%, p = 0.046), while in summer of 2022 trout (6%, p = 0.001), terrestrial insects (5%,p < 0.001), larval Coleoptera (4%, p < 0.001), adult Coleoptera (1%, p = 0.01), and Oligochaeta (2%, p < 0.001) all contributed to differences. In autumn of 2021, Trichoptera (24%, p < 0.001), Gastropoda (15%, p < 0.001), Amphipoda (7%, p < 0.001) and the rare prey group (1%, p = 0.003) contributed to differences. In autumn of 2022, Trichoptera (22%, p < 0.001), Gastropoda (11%, p < 0.001), Amphipoda (9%, p < 0.001) also contributed to diet differences, as well as Isopoda (1%, p < 0.001).

3.4 | 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 < 0.001) and season (F = 34.25, p < 0.001) on $\delta^{15}N$ isotope values, and the effect of species varied by season (species*season; F = 30.29, p < 0.001). There was not a significant effect of year on $\delta^{15}N$ isotope values (p = 0.84). Brown trout were more depleted in $\delta^{15}N$ compared to mottled sculpin in spring (p =0.01) and autumn (p < 0.001), although differences in mean $\delta^{15}N$ values were relatively small, ranging from 0.01‰ to 1.11‰. No significant difference in mean $\delta^{15}N$ was found between the two species in summer (p = 0.08). There was evidence of a significant effect of species (F = 39.53, p < 0.001), season (F = 206.52, p < 0.001), and year (F = 496.94, p < 0.001) on $\delta^{13}C$ isotope values, and the effect of species varied by season (species*season; F = 3.85, p = 0.02). Brown trout were more enriched in $\delta^{13}C$ compared to mottled sculpin in summer (p < 0.001) and autumn (p < 0.001), but no significant difference in mean $\delta^{13}C$ was found between the two species in spring (p = 0.15).

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 estimates ranged from 10% to 40%. In 2021, the highest percent overlap occurred in summer (40%) and the lowest in autumn (10%). While 2022, the highest percent overlap occurred in spring (40%) and the lowest in summer (20%).

4 | DISCUSSION

Resource use by mottled sculpin and juvenile brown trout shifted in alignment with resource availability, where BMI biomass peaked in spring and declined through summer and autumn. Both species for the most part consumed prey items relative to their proportional availability, thus resource availability fundamentally defined feeding opportunities. Mottled sculpin and juvenile brown trout consumed less in autumn, 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 developed more specialized diet patterns instead of increasing diet overlap, resulting in population-level trophic niche expansion in both species. Thus, the population-level trophic niche expansion resulted from increased diet variation between individuals despite individual niche contraction.

These patterns in resource use are consistent with previous studies that have demonstrated that intraspecific competition promotes individual specialization and niche variation within populations (Araújo et al., 2008; Evangelista et al., 2014; Latli et al., 2019; Svanbäck & Bolnick, 2007). For example, Svanback and Bolnick (2007) conducted experiments in which they manipulated threespine stickleback (*Gasterosteus aculeatus*) population density (representative of intraspecific competition) and found that increased intraspecific competition resulted in increased individual specialization and population niche expansion through greater between-individual diet variation. Similarly, a study investigating the impact of habitat homogenization on resource availability and competitive interactions among young-of-year cyprinid species found that decreased resource availability promoted individual specialization and increased diet variation between individuals (Latli et al., 2019). Our findings indicate that increased resource competition in autumn promoted individual specialization and trophic niche partitioning within mottled sculpin and juvenile brown trout populations.

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Our SCA results also revealed significant trophic niche overlap between mottled sculpin and juvenile brown trout across all seasons, indicating these two species utilize similar resources, a pattern commonly observed between juvenile salmonids and cottids (Gabler & Amundsen, 1999; Hannuksela, 1973; Hesthagen et al., 2004). However, the extent of overlap varied seasonally, where overlap peaked in spring, when resources were most abundant, and gradually declined through summer and autumn. 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. These results indicated mottled sculpin and juvenile brown trout partitioned resources to some extent to minimize trophic niche overlap when resources were limited in autumn. Temporal variation in resource use and trophic niche partitioning among fish species has been documented in a variety of studies (Bloomfield et al., 2022; Correa & Winemiller, 2014; Cutting et al., 2016; Falke et al., 2020; Flood et al., 2023; Liu et al., 2019) and is regarded as an important mechanism to minimize competition and facilitate the coexistence of sympatric species especially when resources are limited (Britton et al., 2018; Chesson, 2000; Levine & HilleRisLambers, 2009; Pianka, 1974; Schoener, 1974; Tran et al., 2015).

Interestingly, the reduced trophic niche overlap between mottled sculpin and juvenile brown trout in autumn corresponded to trophic niche expansion for both species. Hence, despite both populations broadening their resource use, brown trout and mottled sculpin were able to increase niche differentiation at the population level. Additionally, as previously mentioned, niche expansion in autumn was driven by increased between-individual diet variation for both species. While several studies have observed decreased trophic niche overlap between species despite the expansion of population niches (Costa-Pereira et al., 2019; Liu et al., 2019; Prati et al., 2021), no 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 populations. Our findings demonstrate that interand intraspecific 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. 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 contradicts 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 stable isotope assimilation time (Bada et al., 2022; Burbank et al., 2019; Futia et al., 2021). As stable isotopes reflect what has been assimilated into an organism tissue, it could represent consumption several weeks to months before sampling (Hesslein et al., 1993; Madigan et al., 2021; Nielsen et al., 2018), whereas SCA provides a "snapshot" of diet composition at the time of sampling. Furthermore, assimilation rates vary with changes in metabolic rates (Matley et al., 2016; Xia et al., 2013). Higher metabolic rates, often associated with warmer temperatures (Clarke & Johnston, 1999; 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 metabolic rates (Fry & Arnold, 1982; Hesslein et al., 1993; 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 a "lag" in assimilation 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 wider niches and reduced overlap in autumn compared to spring.

In conclusion, this study demonstrates the importance of evaluating trophic dynamics at both the indvidual- and population-level to understand seasonal trophic niche overlap among sympatric species. The seasonal fluctuations in trophic niche dynamics emphasizes the need for conducting research with temporal replicates, and might be a key factor contributing to the variation in intra- and inter-specific trophic niche dynamics reported among previous studies (Bloomfield et al., 2022; Costa-Pereira et al., 2017; Cutting et al., 2016; Silva et al., 2014). 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 symptric 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 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.

5 | TABLES & FIGURES

TABLE 1 Total number of individuals (n) within the study size range that were caught and processed (length and weight), and mean ± SD length in mm (FL for brown trout; TL for mottled sculpin), weight in g, Fulton's K (K), energy density (ED), and Stomach Fullness Index (SFI). Vacuity index (VI) and stomach fullness index are in percentages (%). Asterisks denote different sample sizes than (n). Vacuity index and stomach fullness index were calculated for individuals processed for SCA, and energy density was calculated for individuals sacrificed for SIA.

Species	Year	Season	n	Length (mm)	Weight (g)	К	**ED	*VI (%)	*SFI (%)
Brown trout (80 – 200 mm)	2021	Spring	384	105 ± 27	15 ± 13	1.08 ± 0.09	4,223 ± 357	3	0.15 ± 0.24
		Summer	314	115 ± 20	19 ± 13	1.14 ± 0.09	4,544 ± 537	3	0.30 ± 0.43
		Autumn	366	106 ± 29	17 ± 15	1.12 ± 0.08	4,405 ± 590	19	0.06 ± 0.20
	2022	Spring	564	102 ± 26	14 ± 14	1.08 ± 0.09	4,075 ± 908	5	0.15 ± 0.16
		Summer	303	116 ± 22	20 ± 14	1.11 ± 0.12	4,542 ± 526	10	0.11 ± 0.23
		Autumn	193	106 ± 29	17 ± 15	1.12 ± 0.09	4,613 ± 603	17	0.10 ± 0.22
Mottled sculpin (80 – 135 mm)	2021	Spring	300	95 ± 8	14 ± 4	1.54 ± 0.15	4,443 ± 468	11	0.25 ± 0.38
		Summer	297	95 ± 9	13 ± 4	1.47 ± 0.16	4,337 ± 524	7	0.40 ± 1.15
		Autumn	287	93 ± 10	12 ± 4	1.41 ± 0.16	4,246 ± 694	34	0.10 ± 0.47
	2022	Spring	373	93 ± 10	12 ± 5	1.47 ± 0.16	4,054 ± 378	14	0.32 ± 0.76
		Summer	262	94 ± 10	12 ± 4	1.46 ± 0.16	4,115 ± 365	8	0.27 ± 0.49
		Autumn	232	95 ± 9	13 ± 4	1.49 ± 0.16	4,734 ± 2,841	23	0.09 ± 0.33



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 that contributed less than 10% to the diets of brown trout or mottled sculpin were grouped together under the category "Other" for clearer visualization.



FIGURE 2 Mean ± SE proportion of prey in the diets of mottled sculpin and juvenile brown trout, and in the environment, 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 categorized as "miscellaneous" prey.



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 plots (NMDS) of brown trout and mottled sculpin diet in spring (left), summer (center) and autumn (right) in 2021 (top) and 2022 (bottom). Ellipses show 95% confidence intervals. For improved visualization, eight outlier points have been excluded.



FIGURE 5 Seasonal variations in isotopic niches of juvenile brown trout (orange) and mottled sculpin (blue) in spring (left), summer (middle), and autumn (right) in 2021 (top) and 2022 (bottom). Dashed lines correspond to stable isotope ellipse areas (95% CI) and solid lines to standard ellipse areas (40% CI).

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APPENDIX

TABLE S1 Seasonal variation in electivity of prey for mottled sculpin and juvenile brown trout in 2021 and 2022. Electivity values between -0.3 and 0.3 represent neutral selection (0), values > 0.3 indicate preference (+), and values < -0.3 indicate avoidance (-). Prey included: Amphipoda (Amph.), Coleoptera larva (Coleop. L), Coleoptera adult (Coleop. A), Diptera, Ephemeroptera (Ephem.), Gastropoda (Gastro.), Isopoda, Plecoptera (Plecop.), and Trichoptera (Trichop.).

Species	Year	Season	Amph.	Coleop. L	Coleop. A	Diptera	Ephem.	Gastro.	Isopoda	Oligo.	Plecop.	Trichop.
Trout	2021	Spring	_	_	+	0	0	_	_	_	0	0
		Summer	_	-	+	0	0	_	_	_	_	+
		Autumn	_	_	0	0	+	+	_	0	_	_
	2022	Spring	+	_	0	+	0	_	_	_	0	0
		Summer	0	-	+	0	-	0	_	0	_	0
Sculpin	2021	Spring	_	_	_	0	0	_	_	_	0	0
		Summer	+	-	_	0	0	0	_	_	0	0
		Autumn	_	-	_	+	+	0	_	_	_	_
	2022	Spring	+	-	_	0	0	_	_	+	_	_
		Summer	0	-	+	+	0	0	_	0	-	_

Predictor variable	df	SS	R ²	Pseudo-F	p-value
Species	1	6.13	0.016	24.99	0.0001
Season	2	21.76	0.058	44.36	0.0001
Year	1	0.57	0.002	2.31	0.0410
Sample location	4	6.59	0.017	6.72	0.0001
Species * Season	2	5.66	0.015	11.54	0.0001
Residual	1375	337.27	0.89	-	-
Total	1385	377.98	1.00	-	-

TABLE S2 Results of PERMANOVA evaluating differences in diet composition between groups. With species, season, year, an interaction between species and season, and an interaction between season and year included as fixed effects and sample location as a random effect.

TABLE S3 Pairwise PERMANOVA comparison results indicating no size class effect on diet composition for brown trout and mottled sculpin, with one exception (brown trout, spring 2021) (*permanova_pairwise* function in the *ecole* package). Pairwise comparisons were computed with 9,999 permutations and based on a Bray-Curtis similarity matrix. The table includes sum of squares (SS), pseudo-F, R², and Bonferroni adjusted p-values for pairwise comparisons between small (80 – 115 mm) and large (116 – 200 mm) brown trout and small (80 – 95 mm) and large (95 – 135 mm) mottled sculpin across seasons and years.

	Year	Season	SS	Pseudo-F	R ²	p-value
Brown trout	2021	Spring	4.82	27.89	0.11	0.03
		Summer	0.63	3.90	0.04	0.61
		Autumn	0.59	2.03	0.02	1.00
	2022	Spring	1.07	7.99	0.07	0.11
		Summer	0.40	1.52	0.01	1.00
		Autumn	0.80	2.74	0.03	1.00
Mottled sculpin	2021	Spring	0.45	1.81	0.01	1.00
		Summer	1.08	5.21	0.05	0.08
		Autumn	0.27	0.72	0.01	1.00
	2022	Spring	0.38	1.26	0.01	1.00
		Summer	0.38	1.51	0.01	1.00
		Autumn	0.85	2.63	0.03	1.00



FIGURE S1 Mean daily streamflow (in ft³/s) in the Lower Blue River (blue line) compared to an unregulated reference stream, the Eagle River (yellow line), in 2021 (left) and 2022 (right).



FIGURE S2 Seasonal variation in benthic macroinvertebrate (BMI) community composition in the Blue River in spring (left), summer (middle) and autumn (right) of 2021 (top) and 2022 (bottom). BMI that contributed less than 5% to community biomass were categorized as "Other" BMI.



FIGURE S3 Seasonal variation in vacuity index (VI) for juvenile brown trout (left) and mottled sculpin (right) in 2021 (top) and 2022 (bottom).



FIGURE S4 Seasonal variation in stomach fullness index (SFI) for juvenile brown trout (left) and mottled sculpin (right) in 2021 (top) and 2022 (bottom).



FIGURE S5 Seasonal variation in trophic niche overlap between juvenile brown trout and mottled sculpin in 2021 (dark green solid) and 2022 (light green dashed). Values were calculated using Schoener's index of overlap. The dotted line at y = 60 represents the threshold for significant trophic niche overlap.