

Temporal shifts in intraspecific and interspecific diet variation among 3 stream predators

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Abstract: Intraspecific variation is increasingly recognized as an important factor in ecological interactions that can exceed the role of interspecific variation. Few studies, however, have examined how variation in intra- and interspecific resource use affect trophic interactions over time within a seasonally-dynamic food web. We compared diets with respect to predator body size and predator species identity over 3 seasons by collecting stomach contents from 2028 Reticulate Sculpin (*Cottus perplexus*), 479 Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*), and 107 Pacific Giant Salamanders (*Dicamptodon tenebrosus*) in western Oregon streams. In each season, predator body size was strongly associated with dietary composition and positively related to taxonomic breadth and the size of individual prey. Intra- and interspecific diet variation changed substantially across seasons, with much greater interspecific variation in spring than in summer and autumn. Interspecific differences in foraging mode (e.g., benthic vs drift feeding) were associated with predator-specific responses to a seasonal pulse in the availability of terrestrial thrip larvae (Thysanoptera) and contributed to temporal variation in trophic niche differentiation. These findings show that the relative magnitudes of intra- and interspecific diet differentiation can change over time in systems that receive seasonal resource pulses. Our results highlight the dynamic nature of food webs and the need to incorporate sampling over relevant temporal scales to understand species interactions.

Key words: temporal diet variation, intraspecific, predator–prey interactions, food webs, resource pulses, body size, streams

The relative roles of intraspecific and interspecific niche variation in shaping the structure and dynamics of communities remains unclear (May and MacArthur 1972, Schoener 1974, Lichstein et al. 2007, Violle et al. 2012, Hart et al. 2016). Ecologists have largely studied interacting populations at the species level, often ignoring the role of intraspecific variation (Abrams and Ginzburg 2000, Bolnick et al. 2011, Novak et al. 2016). However, individuals within species often differ from one another in ecologically-meaningful ways, including prey preferences (Estes et al. 2003), microhabitat use (Schlosser 1987), vulnerability to predation (Kusano 1981), and competitive ability (Svanbäck and Bolnick 2007). For instance, phenotypic changes that occur throughout ontogeny (e.g., body size, physiology, behavior) often alter the types and strengths of interactions in which individuals participate (Polis 1984, Bolnick et al. 2003, 2011). Indeed, recent empirical studies have demonstrated that intraspecific var-

iation can influence community and ecosystem processes as much as, or even more than, interspecific variation (Des Roches et al. 2018). Thus, emphasis on understanding the mechanisms that drive variation within and among species has been renewed.

A focal point of research on intra- and interspecific variation is their role in species coexistence (Schoener 1974, den Boer 1986, Lichstein et al. 2007, Miller and Rudolf 2011, Nakazawa 2015, Bassar et al. 2017). According to the competitive exclusion principle, species cannot stably coexist if they occupy the same ecological niche because only the differential use of resources permits ecologically-similar species to coexist (Gause 1934, Hutchinson 1957, Chesson 2000). Niche differentiation can be achieved in 3 basic ways: 1) specialization on a distinct set of resources (MacArthur and Levins 1967, Chesson 2000), 2) differential use of resources in space (May and Hassell 1981), or 3) differential

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use of resources in time (Armstrong and McGehee 1980, Chesson 1985). Recent studies have demonstrated the importance of niche differentiation for community dynamics and species coexistence (Hughes et al. 2008, Clark 2010, Jung et al. 2010, Messier et al. 2010, Bolnick et al. 2011, Pruitt and Ferrari 2011, Violle et al. 2012), yet consensus on the underlying mechanisms remains elusive. Some theory suggests that intraspecific variation should promote coexistence (Clark et al. 2003, Hubbell 2005, Fridley et al. 2007, Lichstein et al. 2007), whereas other theory suggests that intraspecific variation is more likely to hinder coexistence (Taper and Case 1985, Hart et al. 2016). Studies that quantify intra- and interspecific variation in both time and space will improve our understanding of species coexistence and its underlying mechanisms.

Researchers are increasingly quantifying intra- and interspecific niche variation, especially variation in resource use (Araújo et al. 2007, Semmens et al. 2009, Coblenz et al. 2017), yet few studies have considered how the 2 forms of niche variation change in relative magnitude over time. Failure to consider time scales may bias inferences regarding the frequency of diet variation within and among species, especially in temporally-variable environments (Woodward et al. 2010, Novak and Tinker 2015). Many aquatic communities experience seasonal changes in community structure, primary production, nutrient dynamics, hydrology, and allochthonous inputs, which often result in temporally-dynamic predator-prey interactions (Closs and Lake 1994, Gasith and Resh 1999, Baxter et al. 2005, Power et al. 2008, Peralta-Maraver et al. 2017, Heng et al. 2018). For instance, seasonal inputs of terrestrial arthropods account for a large portion of available prey for stream predators and can alter foraging habits and diet (Wipfli 1997, Nakano et al. 1999b, Kawaguchi and Nakano 2001, Romero et al. 2005, Li et al. 2016). The response of recipient consumers to resource pulses, however, probably varies with species identity and ecological traits such as body size (Yang et al. 2010), leading to changes in the relative magnitudes of intra- vs interspecific diet variation over time.

In this study, we assessed seasonal changes in the interspecific (i.e., taxonomic identity) and intraspecific (i.e., body size) diet variation of a stream predator guild. We studied 3 generalist predators that co-occur in forested streams throughout western Oregon: Reticulate Sculpin (*Cottus perplexus*), Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*), and Pacific Giant Salamanders (*Dicamptodon tenebrosus*). Reticulate Sculpin are small, benthic fish that primarily consume benthic macroinvertebrates (Bond 1963, Petrosky and Waters 1975, Wydoski and Whitney 1979, Scott and Crossman 1998, Preston et al. 2017). As aquatic larvae, Pacific Giant Salamanders are also benthic but are less specialized predators that consume benthic macroinvertebrates, terrestrial arthropods, and stream-dwelling vertebrates (Kelsey 1995, Cudmore and Bury 2014). In contrast to sculpin and salamanders, Cutthroat Trout are active swim-

mers that feed on terrestrial and aquatic prey both at the water surface and in the benthos (Chapman and Bjornn 1969, Romero et al. 2005, Li et al. 2016).

Given the differences in foraging strategies among our focal predators and the inherent seasonality of mediterranean-climate streams (Gasith and Resh 1999), we hypothesized that the relative magnitudes of intra- and interspecific diet variation would change over time. We addressed this hypothesis by analyzing predator stomach contents with respect to predator body size and predator species identity over 3 seasons. Our results show that associations between diet and both predator body size and predator species identity vary with season. These findings demonstrate the importance of considering both forms of niche variation across time for understanding how trophic interactions influence community dynamics.

METHODS

Data collection

We surveyed 3 stream reaches in each of Soap, Oak, and Berry Creeks (9 total sites) in Oregon State University's McDonald-Dunn Research Forest northwest of Corvallis, Oregon (44.638 N, 123.292 W). The 3 study streams were ~1 to 3 m wide at base flow, flowed through mixed deciduous-coniferous forests into higher order tributaries of the Willamette River, and supported a diverse assemblage of aquatic macroinvertebrates (>325 species; Anderson and Hansen 1987). Each reach was ~45 m long and contained a combination of pool and riffle habitats (typically 2–3 of each habitat type).

To collect stomach contents, we conducted electrofishing surveys during the d (0900–1700) over roughly 2 wk in each summer (June and July 2015), autumn (September 2015), and spring (April 2016). During each survey, a crew of 4 researchers captured predators with a single pass of a backpack electroshocker (Smith-Root LR20B; Vancouver, Washington), a block net (1.0 × 1.0 m), and 2 dip nets (0.30 × 0.25 m). Captured Reticulate Sculpin, Coastal Cutthroat Trout, and Pacific Giant Salamanders were anesthetized with AQUI-S[®] (Lower Hutt, New Zealand) (Silbernagel and Yochem 2016), measured for total length, lavaged non-lethally to collect stomach contents, and released back into the stream following a recovery period in aerated stream water. Most individuals were lavaged with a 60-cc syringe and a blunt 18-gauge needle, but individuals >100 mm were lavaged with a small straw (2.5 mm in diameter) attached to a 500-mL bottle of stream water. We did not lavage individuals of any species smaller than ~25 mm. We preserved stomach contents in 70% ethanol and identified them in the laboratory with a dissecting microscope (8× to 35× magnification) to the lowest possible taxonomic level (usually family) according to Merritt et al. (2008). Total lengths of whole, intact prey items were measured (to the nearest 0.5 mm) to analyze associations between prey size and

predator species identity, predator body size, and season. Additional details about study sites and data collection are provided in Preston et al. (2018, 2019).

Data analyses

To examine the association between diet and predator body size, we subdivided each predator species into size classes based on the distribution of total lengths observed across all seasons. We assigned sculpin and trout to small (<25th percentile), medium (25th–75th percentile), and large (>75th percentile) size classes. The sample size of salamanders was relatively low, so we assigned salamanders into 2 size classes: small (<50th percentile) and large (>50th percentile).

We first quantified overall and seasonal dietary niche breadth at both the species and size-class levels with Levins' (1968) standardized measure (Hurlbert 1978),

$$B_i = \frac{\left[\left(\frac{1}{\sum_{i=1}^n p_{ij}^2} \right) - 1 \right]}{(n - 1)}, \quad \text{Eq. 1}$$

where p_{ij} is the proportion of prey type i in the stomachs of predator group j , and n is the total number of prey items consumed by predator group j . Standardized niche breadth values range from 0 (highly specialized) to 1 (highly generalized). We used the lowest possible taxonomic level of prey identification (as suggested by Greene and Jaksic 1983) and treated different prey life stages (i.e., larval, pupal, adult) as distinct prey types. We estimated niche breadth means and standard errors with non-parametric bootstrapping (1000 draws of 20 prey items) to account for differences in sample sizes among seasons and predator groups.

We then calculated proportional diet composition in each season by dividing the total number of a given prey group found in the stomach contents of a given species (or size class) by the total number of prey items found in the stomach contents of that species (or size class). To reduce complexity in statistical analyses of diet composition, we grouped the prey into 7 categories: Diptera larvae (true flies), Ephemeroptera larvae (mayflies), Trichoptera larvae (caddisflies), aquatic snails (*Juga sp.*), emergent adult insects (i.e., aquatic insects that had emerged from the stream), terrestrial prey (i.e., organisms with no aquatic life stage), and other. The other category accounted for <5% of total prey items. We estimated prey counts rather than prey biomass because our goal was to examine differences in diet composition rather than energetic contributions of prey (Hyslop 1980, Preston et al. 2017). Highly-digested or otherwise unidentifiable prey items were not counted.

We used Bayesian multivariate generalized linear mixed effects models to examine the relationships between the 7 dietary groups and predator body size, predator species, and season. To account for the potential repeated measurement of diets from the same predator individuals at a site, we included random effects of stream reach within stream and of

stream identity. We used a zero-inflated Poisson distribution to model the multivariate prey count data for the 7 prey groups. The multivariate models included fixed effects of predator body size (continuous variable), predator species (3 categories), and season (3 categories). We used the deviance information criterion (DIC) to compare a model with a 3-way interaction between the fixed effects, a model with all possible 2-way interactions, and nested models that dropped each of the 2-way interactions separately (6 total models). The 2-way interactions tested whether the relationships between prey identity and body size differed across seasons, and whether the relationship with body size differed across predator species. Bayesian mixed effects models were implemented with the *MCMCglmm* package in R (version 3.5.2; R Project for Statistical Computing, Vienna, Austria) with the default priors with 40,000 iterations, a burn-in period of 15,000, and a thinning factor of 100 to minimize autocorrelation (Hadfield 2019).

To examine the factors associated with prey size, we used linear mixed effects models that included predator body size, predator species, and season as fixed effects, and individual predator identity, stream reach, and stream identity as nested random effects (Zuur et al. 2009). We included all possible interactions between the fixed effects, including the 3-way interaction. We log-transformed predator and prey body sizes to conform to model assumptions and used likelihood ratio tests to compare the nested models that lacked each of the interactions. Linear mixed effects models were implemented with the *lme4* R package (Bates et al. 2014).

To evaluate how dietary overlap between predators changed over time, we applied a hierarchical cluster analysis on proportional diet compositions of the 7 prey groups and generated dendrograms that depicted dietary dissimilarity among size-classes of each predator species within each season. We used the unweighted pair-group method to cluster dissimilarities in diets measured with Euclidean distance (Ward 1963, Krebs 1989, Amundsen et al. 2003). We supplemented this cluster analysis with higher resolution taxonomic data by calculating dietary overlap among species and size classes within each season with the Schoener index of % overlap,

$$100 \left(1 - \frac{1}{2} \sum_i |p_{xi} - p_{yi}| \right), \quad \text{Eq. 2}$$

where p_{xi} and p_{yi} represent the proportion of prey type i in the stomachs of predator species (or size classes) x and y , respectively. % overlap ranges from 0 (no overlap) to 100% (complete overlap) (Schoener 1970).

RESULTS

In total, we lavaged 2028 sculpin, 479 trout, and 107 salamanders (see Table S1 for numbers of stomachs sampled by size class and season). We found a total of 22,798 identifiable prey items belonging to 104 prey types. We did not

find identifiable prey in 115 sculpin (5.67%), 19 trout (3.97%), and 13 salamanders (12.1%) (Table S1). Diptera larvae and Ephemeroptera larvae were most common and constituted 36.9 and 36.4% of all prey items, respectively (Fig. 1A–C). In general, sculpin and salamander diets were comprised primarily of benthic aquatic invertebrates, whereas trout diets were comprised of a more even mixture of terrestrial, aquatic, and semi-aquatic prey. Trout diets contained the highest overall proportions of adult aquatic insects (9.4%) and terrestrial prey (19.8%). Mean dietary niche breadth (\overline{Bi}) over all seasons combined was lowest (most specialized) in sculpin ($\overline{Bi} = 0.041$; 95% confidence interval [CI] = 0.023–0.059), highest (most generalized) in trout ($\overline{Bi} = 0.078$; 95% CI = 0.043–0.113), and intermediate in salamanders ($\overline{Bi} = 0.062$; 95% CI = 0.033–0.091).

Within each predator species, proportional diet composition and niche breadth varied based on predator size class. Sampled predator body sizes ranged from 27 to 242 mm, with salamanders (47–242 mm) and trout (30–223 mm) spanning a larger size range than sculpin (27–81 mm; Table S1, Fig. S1). For sculpin and trout, Diptera larvae were found in higher proportions in the diets of smaller size classes,

whereas Ephemeroptera larvae were found in higher proportions in larger size classes. Based on proportional diet composition averaged across seasons, large sculpin (61–81 mm) consumed 19.1% fewer Diptera larvae and 19.5% more Ephemeroptera larvae than small sculpin (27–47 mm). Similarly, large trout (107–223 mm) consumed 27.4% fewer Diptera larvae and 11.3% more Ephemeroptera larvae than small trout (30–54 mm). Large trout also consumed higher proportions of adult aquatic insects and terrestrial prey than small trout. Small salamanders (47–95 mm) consumed high proportions of Ephemeroptera larvae, but large salamanders (96–242 mm) consumed more prey that were not Ephemeroptera or Diptera (e.g., snails, crayfish, annelids, and other rare prey). Mean dietary niche breadth was higher in larger size classes within each predator species (Fig. 2A–C). Additionally, cannibalism on smaller individuals was observed in 14 sculpin (13 singletons, 1 doubleton) and 2 trout (both singletons). Predation on sculpin was observed in 2 salamanders (both singletons).

Trout diets exhibited the greatest seasonal variation. This variation included a shift in proportional consumption of terrestrial thrips (Thysanoptera) from <1% in summer and

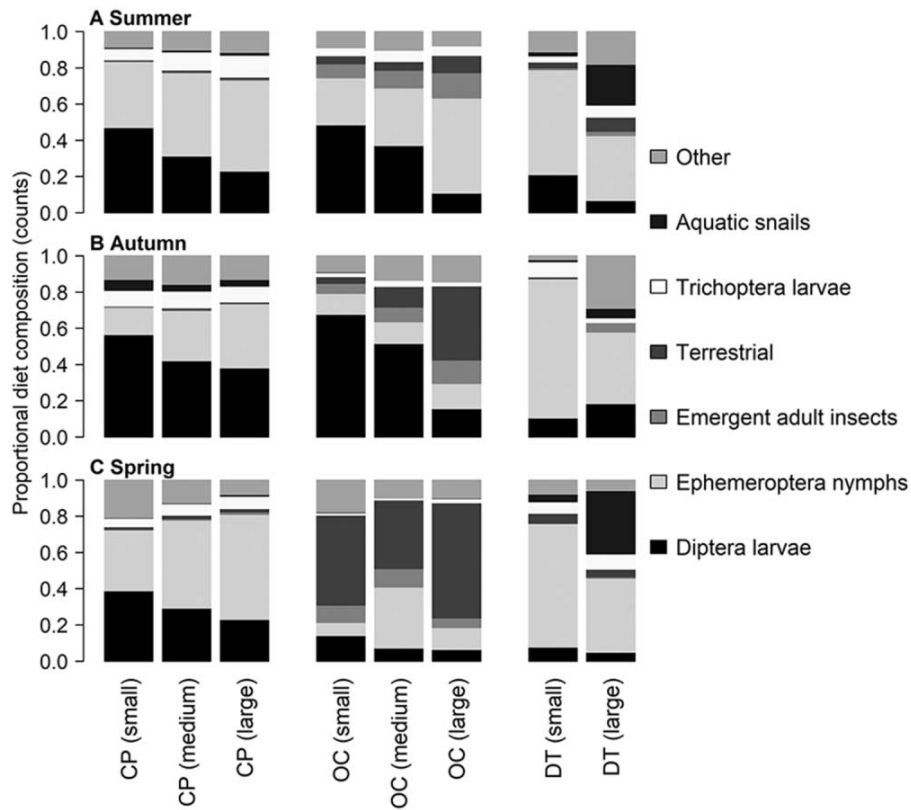


Figure 1. Proportional composition (based on counts) of primary prey groups in the diets of sculpin (CP), trout (OC), and salamanders (DT) in summer (A), autumn (B), and spring (C). Adult stages of aquatic insects are grouped separately from terrestrial organisms without aquatic life stages. The other category is composed of aquatic and semi-aquatic prey that amounted to <5% of the total prey items within predator diets.

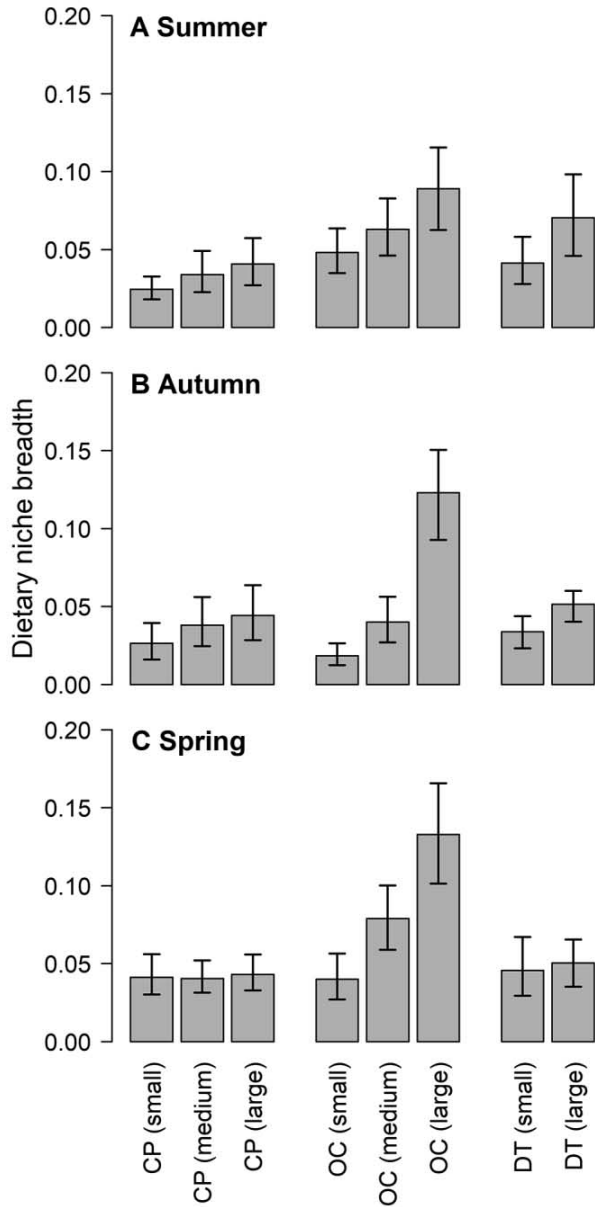


Figure 2. Mean (\pm 95 % confidence interval) dietary niche breadth quantified with Levins' (1968) standardized measure by size class for sculpin (CP), trout (OC), and salamanders (DT) in summer (A), autumn (B), and spring (C). Lower dietary niche breadth values indicate more specialized diets.

autumn to 49.8% in spring. In spring, the consumed thrips were almost entirely larvae, whereas adult thrips were only consumed in summer and autumn. Proportions of Diptera larvae and Ephemeroptera larvae found in trout stomachs were also highly variable across seasons: trout diets contained relatively high and even proportions of Diptera and Ephemeroptera in summer (~35 and ~33%, respectively),

high proportions of Diptera (~52%) and low proportions of Ephemeroptera (12%) in autumn, and low proportions of both in spring (~9 and ~15%; Fig. 1A–C). Trout dietary niche breadth also varied strongly with season from a low in autumn ($\bar{B}_i = 0.049$; 95% CI = 0.023–0.075), intermediate in summer ($\bar{B}_i = 0.067$; 95% CI = 0.047–0.089), and high in spring ($\bar{B}_i = 0.086$; 95% CI = 0.049–0.123).

In contrast, sculpin and salamander diets exhibited little seasonal variation in proportional diet composition and dietary niche breadth, and their diets rarely included thrips (Tables S2–S4). Sculpin dietary niche breadth ranged from low in summer ($\bar{B}_i = 0.034$; 95% CI = 0.019–0.049) to high in spring ($\bar{B}_i = 0.043$; 95% CI = 0.028–0.058). Salamander dietary niche breadth was lowest in summer ($\bar{B}_i = 0.044$; 95% CI = 0.029–0.059) and highest in autumn ($\bar{B}_i = 0.063$; 95% CI = 0.036–0.090).

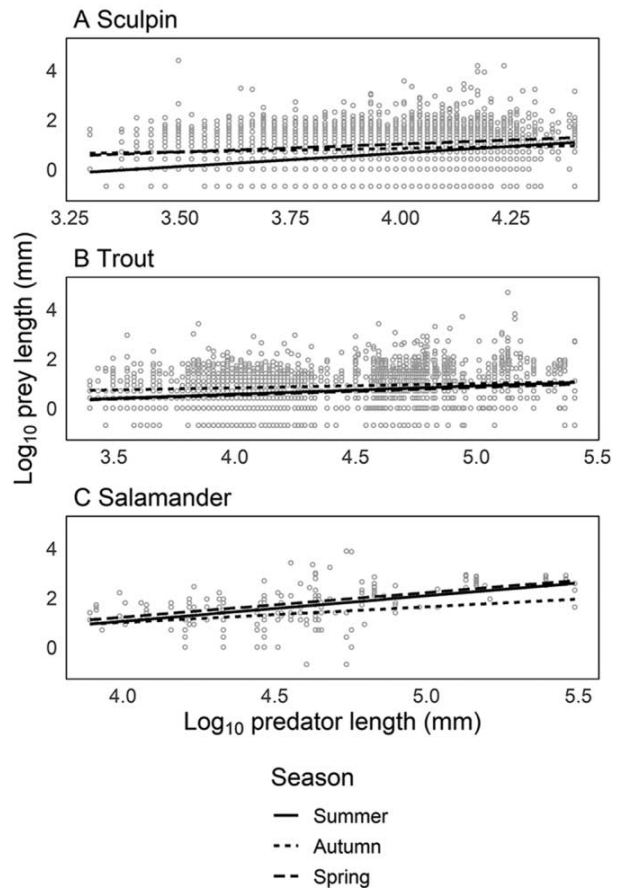


Figure 3. Linear regression plots depicting the relationships between log-transformed total lengths of sculpin (A), trout (B), and salamanders (C) and the log-transformed total lengths of whole intact prey items in their stomach contents. Different lines are fit for summer (solid), autumn (small dashed), and spring (large dashed).

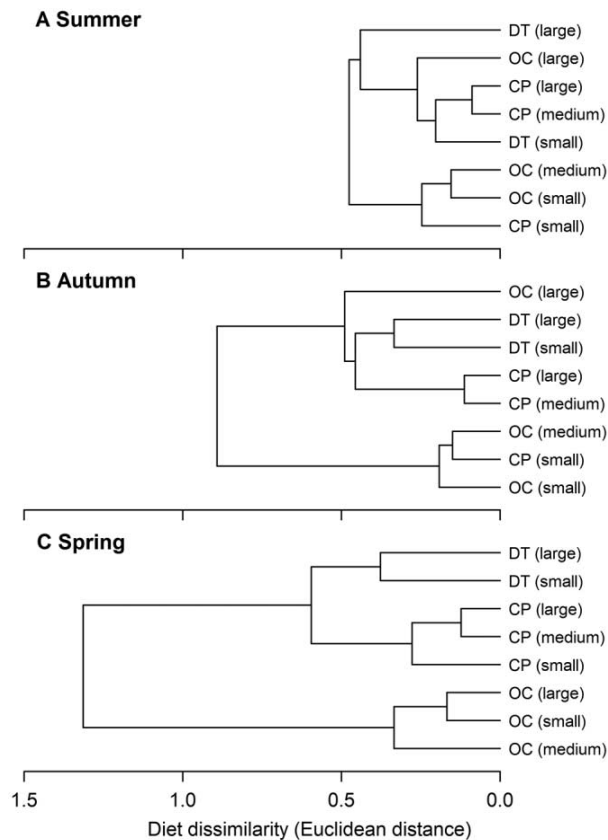


Figure 4. Dendrograms generated from hierarchical cluster analyses of proportional diet composition in size classes of sculpin (CP), trout (OC), and salamanders (DT) in summer (A), autumn (B), and spring (C). Shorter branches represent greater similarity in dietary composition between the connected groups.

The relationships between diet and species identity and body size differed across seasons. For prey composition, the mixed models with all 2-way interactions among fixed effects had the highest relative performance (Tables S6, S7). The 2nd-best model included the 3-way interaction (Δ mean DIC = 17.12). The next best models excluded either the predator body size-by-predator species interaction (Δ mean DIC = 48.95) or the predator body size-by-season interaction (Δ mean DIC = 54.15). Excluding either the predator species-by-season interaction or all 2-way interactions most decreased model performance (Δ mean DIC = 579.79 and 596.73, respectively).

Prey size increased with predator body size (Fig. 3A–C), and this relationship varied across predator species (species \times size: $df = 2$, $\chi^2 = 25.02$; $p < 0.001$) but not across seasons (season \times size: $df = 2$, $\chi^2 = 4.88$; $p = 0.087$). The 3-way interaction was not significant (species \times season \times size: $df = 4$, $\chi^2 = 0.37$; $p = 0.98$). Overall, mean prey length

(\overline{TL}) was much larger in salamanders ($\overline{TL} = 7.6$ mm, $\sigma = 6.7$) than in sculpin ($\overline{TL} = 2.8$ mm, $\sigma = 2.7$) or trout ($\overline{TL} = 2.5$ mm, $\sigma = 2.7$).

Consistent with our other analyses, the hierarchical clustering of diet similarity by size classes varied across seasons (Fig. 4A–C). Diet dissimilarity among size classes was lowest in summer (Fig. 4A), intermediate in autumn (Fig. 4B), and highest in spring (Fig. 4C). In summer and autumn, the diets of heterospecific size-class combinations were often more similar than the diets of conspecific size-class combinations. Size classes were only clustered according to predator species in spring, when sculpin and salamander diets were similar to each other and highly dissimilar to trout diets. The analysis of % overlap between species and size classes was also consistent with other analyses (Table S5). Dietary overlap generally decreased with increased differences in body size within and between species, and trout size classes showed the lowest dietary overlap with sculpin and salamander size classes in spring.

DISCUSSION

The relative difference between intra- and interspecific diet variation changed substantially across seasons, reflecting temporal variation in the relationships between diet and predator body size and species identity. These relationships were driven partly by differences in prey availability. The large increase in magnitude of interspecific diet variation in spring, for instance, was associated with seasonal changes in prey composition, particularly of terrestrial subsidies. Trout diets were comprised of a mixture of terrestrial and aquatic prey but were highly variable across seasons, and their spring diets contained high proportions of terrestrial prey. In contrast, sculpin and salamander diets were comprised primarily of benthic aquatic prey and showed relatively low seasonal variation. This seasonal difference in diet variation is consistent with previous studies that show that seasonal diet shifts are ubiquitous among freshwater salmonids but are not widely observed in sculpin or salamanders (Wilhelm et al. 1999, Romero et al. 2005, Li et al. 2016, Cochran-Biederman and Vondracek 2017). Prey-specific sculpin feeding rates are also relatively consistent across space and time in our study streams (Preston et al. 2019), especially compared to the more variable trout diets observed in the present study.

Differences in dietary niche breadth among our focal predators also stemmed from differences in foraging strategies. Sculpin and salamanders are bottom-dwelling ambush predators that feed primarily on benthic macroinvertebrates (Bond 1963, Daniels and Moyle 1978, Kratz and Vinyard 1981, Wells 2007, Cudmore and Bury 2014). In contrast, Cutthroat Trout are active swimmers that have a wider diet breadth because they feed on both the benthos and throughout the water column, and they commonly consume terrestrial prey (Chapman and Bjornn 1969, Romero et al. 2005, Li

et al. 2016). Trout diets are therefore expected to exhibit greater responses to changes in terrestrial prey availability than are sculpin and salamander diets. Further, the strong seasonality in terrestrial prey subsidies compared to the relative consistency of the benthic prey assemblage in our study streams (Preston et al. 2018) led to even stronger relative seasonality in trout diets. These species-specific responses to changes in prey assemblages are consistent with prior experimental work. For example, stream predators respond to changes in the availability of terrestrial prey in a species-specific manner based on differences in their diet breadth and foraging behavior (Gillette 2012). Riparian consumers also exhibit species-specific responses when aquatic-derived subsidies are manipulated (Paetzold et al. 2006, Marczak and Richardson 2007). Taken together, these results emphasize how the interplay of predator characteristics (e.g., diet breadth and foraging behavior) and prey characteristics (e.g., seasonal changes in availability) can interact to drive temporal shifts in the relative importance of intra- and interspecific diet variation.

The high seasonal variation in trout diets was driven largely by their consumption of western flower thrips, *Frankliniella occidentalis*. Larval thrips comprised nearly 1/2 of all prey consumed by trout in spring but <2% of sculpin and salamander diets. Moreover, the complete absence of larval thrips in stomach contents in summer and autumn suggests that thrip availability to stream predators is highly seasonal. Thrips are widespread agricultural pests that hatch annually from eggs in plant tissues and later drop to the ground before metamorphosing into adults (Sanderson 1990, Teulon et al. 1993). The timing of the thrip lifecycle is temperature dependent, with the larval stage lasting just 5 to 20 days. Thus, larval thrips apparently dropped from overhanging canopy into our study streams prior to or during the spring surveys and were subsequently consumed at disproportionately high rates by trout compared to sculpin and salamanders. Previous evidence of thrip consumption by stream predators is scarce but has been documented in Brook Trout (Williams 1981) and sticklebacks (Hynes 1950). However, similar pulsed inputs of terrestrial arthropods occur in forested streams and contribute a large portion of available prey for stream predators (Wipfli 1997, Nakano et al. 1999b, Kawaguchi and Nakano 2001, Nakano and Murakami 2001, Kawaguchi et al. 2003, Baxter et al. 2005, Romero et al. 2005, Li et al. 2016). Our results demonstrate how a temporal resource pulse in even a single allochthonous prey taxon could reshape predator-prey interactions.

Predator body size had strong and relatively-consistent associations with diet composition. In all seasons, we found shifts in the relative proportions of prey groups in stomach contents as well as increases in both dietary niche breadth and prey size with increasing predator body size. Body size is a key trait that dictates an organism's trophic ecology and interactions with its environment (Werner and Gilliam 1984, Woodward and Warren 2005, Woodward et al. 2005, Pet-

chey et al. 2008, Rudolf et al. 2014). For instance, prey consumption within a guild of stream predators can be driven primarily by body-size constraints that limit predation to a subset of the prey-size spectrum (Woodward and Hildrew 2002). Here, we found that dietary overlap was generally higher between groups of similar body size and, in several cases during summer and autumn, dietary overlap was higher between heterospecifics of similar body size than between conspecifics of different body size (Table S5). For example, in both summer and autumn, the diets of small trout and small sculpin overlapped more than the diets of small sculpin and large sculpin. In spring, however, trout diets were highly dissimilar from sculpin and salamander diets, and dietary overlap between small sculpin and small trout was <1/2 the overlap between small and large sculpin. This substantial shift in dietary overlap across seasons reflects temporal variation in the relationships between diet composition and body size and species identity, which was driven by trout consumption of thrips in spring.

Temporal variability in the relative magnitudes of intra- and interspecific variation may promote the coexistence of our focal predators by limiting similarity in resource use over time. According to coexistence theory, increased dissimilarity in resource use should lead to decreased competition (MacArthur and Levins 1967, Barabás et al. 2018). Thus, seasonal shifts in intra- and interspecific diet variation, such as those caused by the temporal pulse of larval thrips in our study, may coincide with changes in the strength of competition (Zaret and Rand 1971, Chase and Leibold 2003, Correa and Winemiller 2014, Neves et al. 2018). For instance, Zaret and Rand (1971) suggest that decreased interspecific competition during the wet season, when food resources in tropical streams are high, explains seasonal diet shifts in characin fishes. Such temporal variation in resource partitioning may be a key mechanism that facilitates coexistence of stream predators (Nakano et al. 1999a, Dineen et al. 2007). Our inferences of dietary niche differentiation are limited because we used counts in diet analyses rather than biomass, which would better approximate energetic contributions of prey, and we did not estimate feeding rates or quantify prey availability. Further, we were unable to infer the strength of competition in our system with the collected data because species that overlap in resources do not necessarily compete (Menge 1979), competition may occur along multiple niche dimensions beyond diet (Pianka 1975), and patterns of niche overlap may reflect "ghosts of competition past" (Connell 1980). Our study nevertheless supports the hypothesis that the relative magnitudes of intra- and interspecific diet variation change over time. Future research is needed to link these shifts in intra- and interspecific diet variation to temporal changes in the strength of competition.

Seasonality in environmental factors and the strength of predator-prey interactions is widespread (Ostfeld and Keesing 2000, Woodward et al. 2010, Thompson et al. 2012,

Humphries et al. 2017, Calizza et al. 2018), with temporal variation in the relative magnitudes of intraspecific and interspecific diet variation probably occurring in most food webs. Temporal pulses in the availability of even a single prey type are common and occur across various time scales (Yang et al. 2010). Examples include diurnal pulses of marine copepods consumed by pelagic fishes (Godin 1981), annual pulses of anadromous fish carcasses consumed by minks (Ben-David 1997), and multiannual fluctuations in abundances of rodents consumed by owls (Korpimäki 1992). Increasing interest in understanding the role of pulsed resource dynamics in ecological processes emphasizes the need to conduct trophic studies on time scales that match the relevant intrinsic and extrinsic drivers, such as seasonal variation in prey assemblages (Yang et al. 2008). We recommend that future studies of trophic interactions and species coexistence should consider temporal resource pulses and incorporate time scales that are relevant to the life histories of the interacting species.

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