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Individual-level data reveal high prevalence of positive size-trophic position relationships for vertebrates in temperate streams

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Abstract

1. A positive relationship between body size and trophic position is often assumed in ecology, but efforts to confirm the generality of this relationship for freshwater vertebrates have produced mixed results. Some authors have tested for among-species relationships, using species-level estimates of average size and trophic position. Others have used individual-level body size and trophic position data to test for within-species relationships. However, no study has yet estimated *prevalence*, defined here as the fraction of total standing stock biomass within a given ecosystem that consists of taxa exhibiting positive size versus trophic position relationships.
2. Individual-level estimates of body size and relative trophic position (inferred from bulk-tissue nitrogen stable isotopes) were collected for vertebrates in six temperate streams. In each stream, all locally occurring vertebrate taxa were collected and closed population depletion samples were used to obtain standing stock biomass estimates.
3. Ordinary least squares regression was used with the individual-level data to test for positive relationships between body size and relative trophic position (*r*-STPRs). A separate *r*-STPR model was tested for each vertebrate species collected at the six study sites. Linear mixed-effects modelling was then used to test for differing *r*-STPRs among species.
4. Prevalence of the *r*-STPR was calculated for each site by summing the standing stock biomass of all taxa that exhibited a statistically significant, positive STPR at a given site, then dividing this number by the total standing stock biomass of vertebrates at the site.
5. Significant, positive *r*-STPRs were detected in 15 of 22 species × site regression models. Prevalence of species with positive *r*-STPRs ranged from 91 to 100% of the total vertebrate biomass in western streams and from 45 to 66% in eastern streams.
6. Results confirm that positive *r*-STPRs are characteristic of many of the vertebrate taxa considered in this study. Furthermore, species that exhibit positive *r*-STPRs comprise a clear majority of the standing stock biomass in five of six study streams. By using individual-level data to account for prevalence, a more complete

understanding of size-dependent trophic dynamics should be possible in freshwater ecosystems.

KEYWORDS

^{15}N stable isotope, biomass, linear regression, size-selective predation, stream fishes

1 | INTRODUCTION

Body size is fundamental to many physiological and ecological processes, ranging from individual metabolism and growth rate to the regulation of population density and production (Brown et al., 2004; Peters, 1983). Because body size is predicted to increase with trophic position (Elton, 1927), it also plays a central role in predator–prey and food web theory (Arim et al., 2010; Brose et al., 2019; Cohen et al., 1993). For instance, if predators and their prey adhere to a predictable body size–trophic position relationship (STPR), complex ecosystems can be summarised by relatively simple models, such as trophic pyramids (Trebilco et al., 2013).

Efforts to document STPRs for aquatic vertebrates have often focused on among-species comparisons, in which each species is represented by a single, average body size and average trophic position estimate. Multiple species' averages are then combined to test for an overall STPR. So far, results from among-species studies have been mixed. Some studies report strong evidence for positive STPRs (e.g. Dantas et al., 2019). Some report conditional outcomes, with significant, positive STPRs detected for specific sub-groups of aquatic vertebrates (e.g. Potapov et al., 2019; Riede et al., 2011; Romanuk et al., 2011). Others report no evidence for positive STPRs (e.g. Layman et al., 2005).

Tests for positive STRPs have also been conducted within species. These tests use individual-level estimates of body size and trophic position, collected across a range of sizes, to track changes throughout a species' life history (Mittelbach et al., 1988; Trebilco et al., 2013; Woodward & Warren, 2007). Such tests may be particularly instructive because species-level averages can obscure STPRs for stage-structured organisms that experience ontogenetic shifts in feeding behaviour (Mittelbach & Persson, 1998; Osenberg et al., 1994; Werner & Gilliam, 1984). Using individual-level data, some authors have reported strong evidence of positive STPRs for aquatic vertebrates (e.g. Fraley et al., 2020; Jacobi et al., 2020), while others have reported significant STPRs for some, but not all species (e.g. Fry et al., 1999; Keppeler et al., 2020).

One dimension of the STPR debate that has not yet been addressed is the relative abundance or biomass of individuals that adhere to positive STPRs. The concept is herein labelled *prevalence* and defined as the fraction of total standing stock biomass, within a given ecosystem, that consists of individuals exhibiting positive STPRs. Prevalence testing necessarily requires individual-level data, collected for all co-occurring species within a system. Individual estimates of size and trophic position are used to test the STPR at the species-level. Species-level results are then compiled at the community-level. In this way, prevalence is a hybrid concept in STPR research; it integrates within- and among-species results.

When the biomasses of co-occurring taxa are similar, prevalence will be likely to reflect traditional STPR results. For example, in a theoretical community where half of the resident species exhibit positive STPRs and biomass is evenly distributed among species, prevalence will be *c.* 0.5. However, in a community where biomass is dominated by a few taxa, the prevalence of positive STPRs will depend upon the abundances and/or sizes of individuals within the community. Prevalence and the functional importance of the STPR may therefore be high in a system where only one or several taxa exhibit a positive STPR, so long as these taxa comprise a large fraction of the total biomass.

This study explores STPR prevalence within freshwater ecosystems, using aquatic vertebrates from temperate streams in the eastern and western U.S.A. as model systems. Two specific questions are addressed: (1) Are positive STPRs common among vertebrate taxa when individual-level body size and trophic position estimates are examined? and (2) Is STPR prevalence for aquatic vertebrates high or low in temperate streams? To answer these questions, original body size and nitrogen stable isotope data were collected for vertebrates in each of six study streams. Sampled vertebrates included all locally occurring fishes and primarily aquatic amphibians. Regression models of the STPR were then tested separately for each vertebrate taxon within a given stream, using the nitrogen stable isotope data as a proxy for trophic position. Finally, system-level prevalence was estimated at each site by calculating total standing stock biomass (individuals of all species combined), then comparing it with the summed biomass of taxa that exhibited a significant, positive STPR.

2 | METHODS

2.1 | Study sites

Vertebrates were sampled from three eastern U.S. streams in July 2017 and from three western U.S. streams in July 2018 (Figure 1). Falls Creek is a second-order tributary to the Chuwach River (Columbia River Basin) in Okanogan County, Washington (48.646°N; −120.165°W; 876 m above sea level [a.s.l.]). It is a high elevation desert stream within the Okanogan National Forest. Lookout Creek is a fourth-order tributary to the McKenzie River (Columbia River Basin) in Lane County, Oregon (44.231°N; −122.218°W; 534 m a.s.l.). It flows through old-growth coniferous forest and lies within the H.J. Andrews Experimental Forest. Sagehen Creek is a second-order tributary to the Truckee River in Nevada County, California (39.431°N;

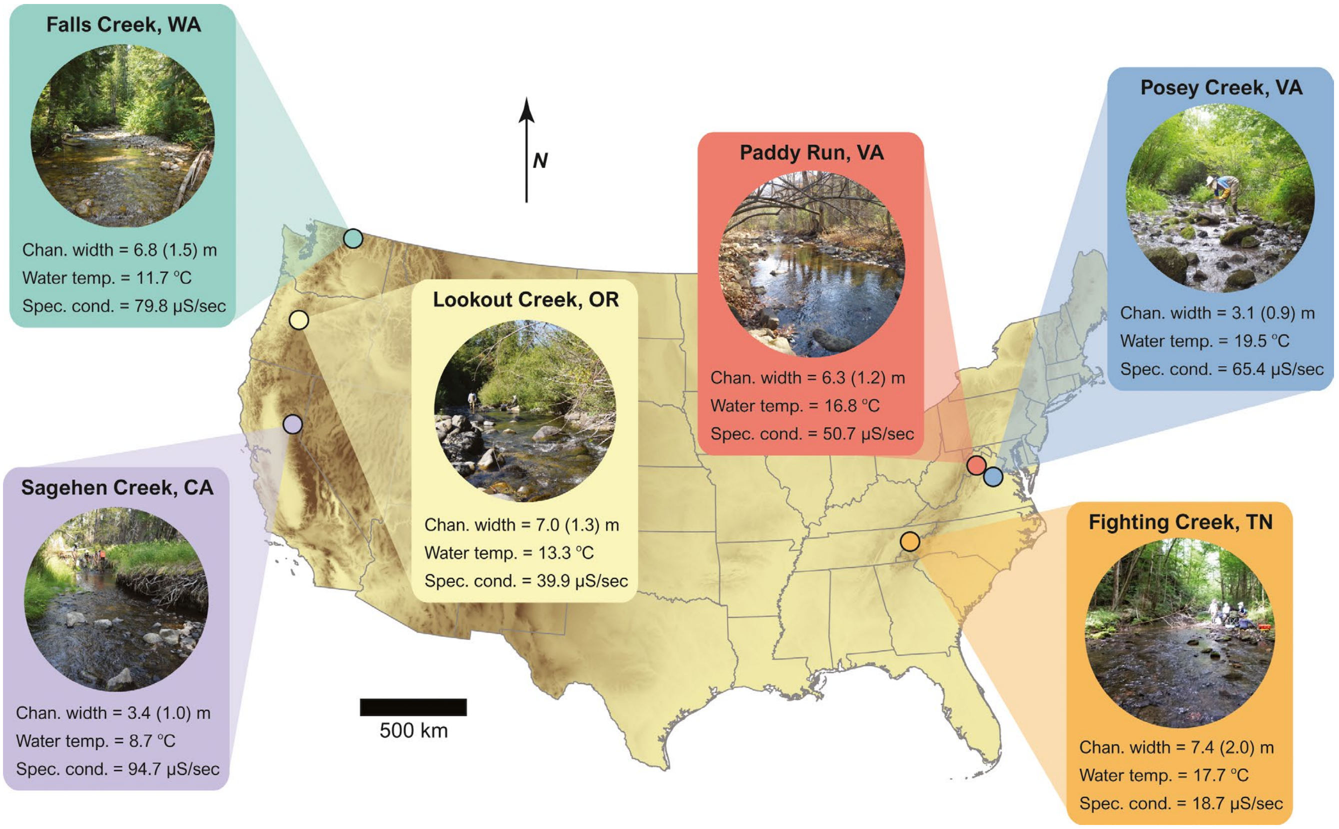

FIGURE 1 Map of the six study streams. Site locations are indicated by the six coloured circles. A representative photo of each stream is included with basic descriptive information, including wetted channel width, water temperature, and specific conductance. Channel width is the mean of 10–20 measurements (±1 *SD*) collected at each site. Temperature and conductance values are instantaneous summer measurements, collected in situ with an electronic meter

−120.241°W; 1937 m a.s.l.). It is an alpine meadow stream that flows through the Sagehen Creek Field Station. Paddy Run is a second-order tributary to the North Fork Shenandoah River (Potomac River Basin) in Frederick County, Virginia (39.056°N; −78.512°W; 434 m a.s.l.). It is a deciduous forest stream within the George Washington National Forest. Posey Creek is a second-order tributary to the South Fork Shenandoah River (Potomac River Basin) in Warren County, Virginia (38.893°N; −78.147°W; 244 m a.s.l.). It lies within the Smithsonian Conservation Biology Institute campus and is a node in the National Ecological Observatory Network. Fighting Creek is a third-order tributary to the Little Pigeon River (Tennessee River Basin) in Sevier County, Tennessee (35.686°N; −83.541°W; 447 m.a.s.l.). It lies near the northcentral margin of Great Smoky Mountains National Park. Substrate within each stream was predominantly boulder and cobble, with isolated reaches of gravel and sand. Silty, depositional areas were observed at only one site (Posey Creek, VA). All study streams flow through forested catchments where anthropogenic disturbance is minimal.

2.2 | Vertebrate and stable isotope samples

At each site, block nets were secured at the upstream and downstream ends of a 100–200 m sampling reach, with longer reaches used in wider streams. A 3-pass depletion survey was then performed in each stream with a 5-person crew and a Halltech HT-2000 backpack electrofisher. Stunned vertebrates were netted and transferred to an aerated holding tank. Each captured specimen was identified to species, weighed as wet mass, and measured for total length.

Next, a stratified random sample of the captured individuals was selected for stable isotope analysis. For each vertebrate species that was represented by at least five individuals captured at a given site, four equal-interval size classes were established in situ that spanned the minimum to maximum range of observed total lengths. Up to 10 individuals were then randomly selected within each size class, euthanised in a lethal dose of Tricane-S (Syndel Laboratories), frozen and returned to the laboratory. All vertebrate sampling methods were approved by the Institutional Animal Care and Use Committee of Virginia Commonwealth University (IACUC permit AD10001331).

In the laboratory, specimens were thawed, oven-dried at 60°C for 48 hr, then weighed whole (mg dry mass). For each of the dried specimens, a sample of dorsal muscle tissue (i.e., white muscle; see Pinnegar & Polunin, 1999) was collected, ground to a fine powder with mortar and pestle, then encapsulated in tin. Oven-dried specimens weighing <100 mg dry mass were excluded because it was difficult to obtain sufficient sample material (≥0.5 mg ground tissue). All encapsulated samples were shipped to the Stable Isotope Facility

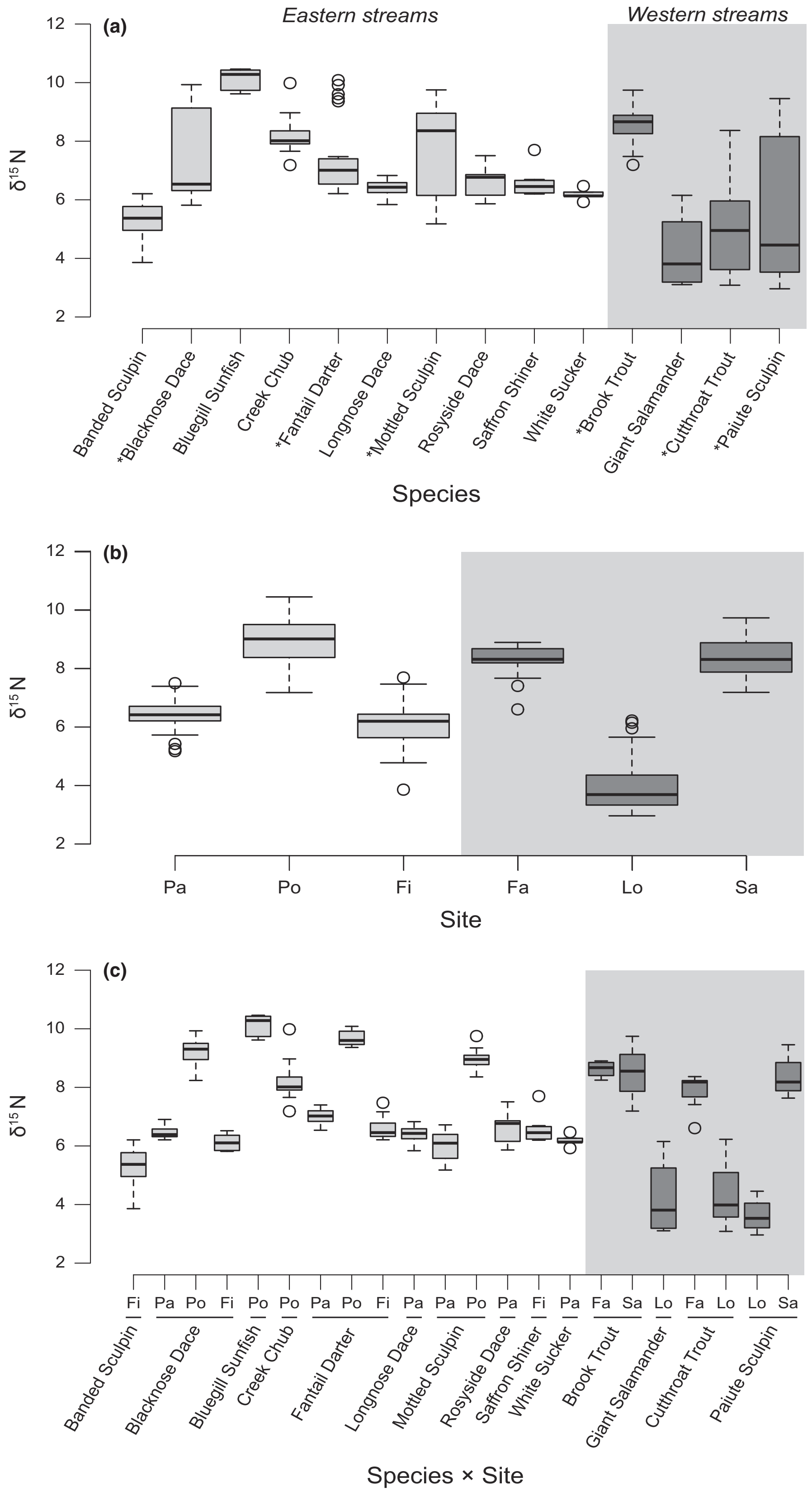

FIGURE 2 Boxplots of the $\delta^{15}N$ data. Results are grouped by species in panel (a), with $\delta^{15}N$ data from multiple sites included for some species (indicated by *), and by study site (data for multiple species combined at each site) in panel (b). Separate $\delta^{15}N$ data are shown for each species × site combination in panel (c). Study sites are identified by the following codes: Pa, Paddy Run, Virginia; Po, Posey Creek, VA; Fi, Fighting Creek, Tennessee; Fa, Falls Creek, Washington; Lo, Lookout Creek, Oregon; Sa, Sagehen Creek, California. In each panel, the western U.S. streams are distinguished from the eastern U.S. streams by grey background shading

at the University of California, Davis for bulk-tissue nitrogen stable isotope analysis.

Reported bulk ^{15}N:^{14}N ratios ($\delta^{15}N$) were then used as indicators of trophic position in STPR models, rather than direct estimates of trophic position per se. This distinction is important because two additional pieces of information are needed to infer trophic position from $\delta^{15}N$: a baseline $\delta^{15}N$ value to set a common point of reference between the $\delta^{15}N$ scale and the trophic position scale, and a trophic fractionation value to predict the increase in trophic position that is expected with a per-unit increase in δ^{15}N (Post, 2002). Without independently confirmed trophic baselines and fractionation values for the six study streams, data analyses were limited to the bulk-tissue δ^{15}N results. However, this was not a problem in STPR modelling because the conversion from δ^{15}N to trophic position is a linear rescaling, analogous to the conversion between °F and °C. This means that the intercepts of STRP regression models (see *Data analysis* below) are dependent on the decision to use one scale or the other, but the model slopes are not. Thus, when testing for covariance between trophic position and another variable such as body size, or predicting a relative change in trophic position, bulk δ^{15}N data can be used directly. It is in this context—detecting and estimating relative changes in trophic position with increasing body size—that δ^{15}N is used herein. Nevertheless, to emphasize the difference between bulk-tissue δ^{15}N and direct trophic position estimates, the STPR is hereafter referenced as the *relative* STPR (*r*-STPR).

2.3 | Data analysis

Prior to analysis, the oven-dried masses were $\log_{10}$ transformed to improve normality. Ordinary least squares regression was then used to model the *r*-STPR, treating δ^{15}N as the dependent variable and $\log_{10}$ dry mass as the independent variable. Each *r*-STPR model tested the null hypothesis that the least squares regression slope did not differ from zero (no significant *r*-STPR) against the 1-sided alternative of a positive slope (trophic position increases with body size). Because all tests were 1-sided, the *p*-values reported for the traditional 2-sided *t*-statistic in the regression results were divided by 2.

A separate species × site *r*-STPR model was built for every vertebrate species with ≥ 5 δ^{15}N samples from a given site, with an exception made for the Coastal Giant Salamander (*Dicamptodon tenebrosus*) in Lookout Creek. The sampling permit for Lookout Creek was limited to four harvested individuals of *D. tenebrosus* (one in each of four size classes). However, this large predator (Parker, 1993) accounted for almost 50% of the vertebrate standing stock biomass in Lookout Creek. Including it in the *r*-STPR models and prevalence analysis was therefore important.

Linear mixed-effects modelling was also used with a pooled dataset (all species and sites combined) to test for significant among-species differences in model slopes (fixed effect) while controlling for the random effect of study site (random intercept). Study site was treated as a random effect because δ^{15}N baselines were highly variable among sites (see RESULTS and Figure 2) and multiple species were included from each site, violating the assumption of statistical independence. Likelihood ratio tests were used with the χ^2 statistic to assess the significance of fixed effects in nested model comparisons (Morrell, 1998). Statistical modelling was performed with R Statistical Software version 3.6.1 (R Core Team, 2019) and the *lme4* package (Bates et al., 2015). Raw data and R code to recreate the *r*-STPR models (least squares and mixed-effects) are available online (see *Data availability* statement).

To estimate prevalence, each species collected at a given site was assigned to one of three categories, based on the respective species × site *r*-STPR model (least squares regression) result: (1) significant, positive slope; (2) non-significant result; or (3) untested due to low sample abundance ($n < 5$). Prevalence of positive *r*-STPRs was then calculated as the summed biomass of category 1 species at a site divided by the total standing stock biomass at that site (categories 1, 2, and 3 combined). Biomass was estimated for each species at a site as the sum of individual dry mass estimates. Total standing stock biomass at a site was then estimated as the sum of the species-level biomass estimates at that site.

For consistency, each of the biomass estimates used in prevalence calculations was inferred from the original field data, after converting individual wet mass to dry mass with the conversion factor of Waters (1977; 1.0 g wet = 0.2 g dry). Oven-dried weights were used in *r*-STPR models, but not to calculate standing stock biomass, because the oven-dried individuals ($n = 301$) comprised only a small fraction of the total number of individuals that were included in the standing stock biomass estimates ($n = 2{,}516$). Using the Waters (1997) conversion factor in standing stock biomass estimates ensured that any bias in the wet-to-dry conversion was uniformly distributed among all prevalence results.

3 | RESULTS

Observed $\delta^{15}N$ values ranged from 2.96–10.46 and were highly variable among species (Figure 2a). Variation in δ^{15}N was also high within some species, such as Blacknose Dace (*Rhinichthys atratulus*) and Paiute Sculpin (*Cottus beldingii*), but this was an artifact of differing δ^{15}N baselines among study sites. Three distinct δ^{15}N baselines were likely to be detected among the six study sites: a low δ^{15}N baseline (median = 3.69) in Lookout Creek; an intermediate baseline (median = 6.33) in Paddy Run and Fighting Creek; and a high baseline (median = 8.66) in Posey Creek, Falls Creek, and Sagehen Creek (Figure 2b). When this δ^{15}N baseline variation was accounted for, using specific species × site combinations of the δ^{15}N data, the within species variation observed in Figure 2a was greatly reduced (Figure 2c).

Samples sizes were adequate (including the exception for Coastal Giant Salamander; see *Data analysis* above) to build 22 individual-level, species × site *r*-STPR models. Of these, 15 exhibited significantly positive slopes (1-sided $p \le 0.05$; see Table 1). *r*-STPRs were most evident in western U.S. streams where significant, positive slopes were observed for all modeled species (Figure 3). In eastern streams, 8 of 15 *r*-STPR model slopes were significantly positive. Among all streams and species, *r*-STPR slopes ranged from 0.49 for the White Sucker (*Catostomus commersonii*) to 2.80

TABLE 1 Results from ordinary least squares regression models predicting δ^{15}N as a function of $\log_{10}$ individual dry mass. For each model, the sample size (*n*), range of body sizes (min − max) in g dry mass, coefficient of determination (r^2), and *p*-value from a one-sided *t*-test of the slope is reported. Slope and intercept estimates are shown with their corresponding standard errors in parentheses (±1 *SE*). Slope estimates are directly comparable among all models, but intercept estimates are not; intercepts are scaled differently among study sites because the δ^{15}N data are influenced by variable δ^{15}N baseline values at each site. Superscript labels A–F are therefore shown with the intercepts to indicate results that are from the same sites and therefore directly comparable

Site	Species	*n*	Size range	r^2	*p*	Slope	Intercept
Falls Creek, WA	Brook trout (*Salvelinus fontinalis*)	11	4.59–18.94	.579	.003	1.213 (0.345)	3.756 (1.385)^{A}
	Cutthroat trout (*Oncorhynchus clarkii*)	9	0.24–20.60	.782	.001	0.785 (0.157)	5.009 (0.577)^{A}
Lookout Creek, OR	Coastal giant salamander (*Dicamptodon tenebrosus*)	4	1.54–17.28	.812	.049	2.803 (0.954)	−6.299 (3.600)^{B}
	Cutthroat trout	33	0.10–11.55	.831	<.001	1.270 (0.103)	0.709 (0.300)^{B}
	Paiute sculpin (*Cottus beldingii*)	32	0.15–2.26	.805	<.001	1.103 (0.099)	0.514 (0.282)^{B}
Sagehen Creek, CA	Brook trout	20	0.13–23.95	.819	<.001	0.929 (0.103)	5.403 (0.353)^{C}
	Paiute sculpin	31	0.10–3.23	.660	<.001	0.931 (0.124)	5.712 (0.357)^{C}
Paddy Run, VA	Blacknose dace (*Rhinichthys atratulus*)	16	0.10–1.07	.029	.264	0.094 (0.145)	6.209 (0.363)^{D}
	Fantail darter (*Etheostoma flabellare*)	10	0.10–0.49	.309	.048	0.607 (0.321)	5.626 (0.731)^{D}
	Longnose dace (*Rhinichthys cataractae*)	14	1.34–6.63	.027	.288	0.196 (0.340)	5.741 (1.179)^{D}
	Mottled sculpin (*Cottus bairdii*)	12	0.22–3.08	.918	<.001	1.379 (0.130)	1.924 (0.388)^{D}
	Rosyside cace (*Clinostomus funduloides*)	8	0.37–1.42	.866	<.001	2.143 (0.345)	0.512 (0.985)^{D}
	White sucker (*Catostomus commersonii*)	5	5.08–25.05	.697	.039	0.490 (0.187)	4.208 (0.754)^{D}
Posey Creek, VA	Blacknose dace	14	0.10–0.78	.245	.036	−0.723 (0.366)	10.967 (0.901)^{E}
	Bluegill sunfish (*Lepomis macrochirus*)	5	0.83–5.42	.282	.179	0.614 (0.566)	8.185 (1.777)^{E}
	Creek chub (*Semotilus atromaculatus*)	15	0.58–33.14	.370	.008	0.782 (0.283)	5.457 (1.000)^{E}
	Fantail darter	5	0.10–0.46	.105	.298	0.330 (0.557)	8.943 (1.263)^{E}
	Mottled sculpin	13	0.25–2.24	.514	.003	0.841 (0.247)	6.427 (0.741)^{E}
Fighting Creek, TN	Banded sculpin (*Cottus carolinae*)	17	0.11–2.32	.679	<.001	1.536 (0.273)	0.890 (0.797)^{F}
	Blacknose dace	8	0.16–1.20	.292	.084	0.534 (0.340)	4.764 (0.867)^{F}
	Fantail darter	10	0.17–0.70	.552	.007	1.391 (0.443)	3.156 (1.102)^{F}
	Saffron shiner (*Notropis rubricroceus*)	9	0.25–0.59	.012	.390	−0.376 (1.294)	7.533 (3.357)^{F}

for the Coastal Giant Salamander (Table 1). Nested comparisons of mixed-effects models (likelihood ratio tests for pooled data) confirmed the overall significance (χ^2 $p \le 0.05$) of dry mass as a key predictor of δ^{15}N (first comparison, Table 2). Subsequent tests confirmed significant differences (χ^2 $p \le 0.05$) among species in model intercepts (second comparison, Table 2) and model slopes (third comparison, Table 2).

Prevalence of positive *r*-STPRs was consistently high in western streams, ranging from 0.91 to 1.00 (Figure 3). Prevalence was lower in eastern streams, where it ranged from 0.45 to 0.66.

4 | DISCUSSION

To my knowledge, this study is the first to estimate the biomass prevalence of positive *r*-STPRs. Confirmed prevalence was >0.90 in each western stream and ≥0.45 in each of the eastern streams. Although novel, these results are not entirely surprising. Many aquatic vertebrates feed upon smaller invertebrate and/or vertebrate prey that are readily available in temperate streams (Allan, 1981; Angermeier, 1982; Meehan, 1996; Rosenfeld, 2000). As these vertebrate predators grow, ontogenetic shifts from lower-to-higher trophic level prey

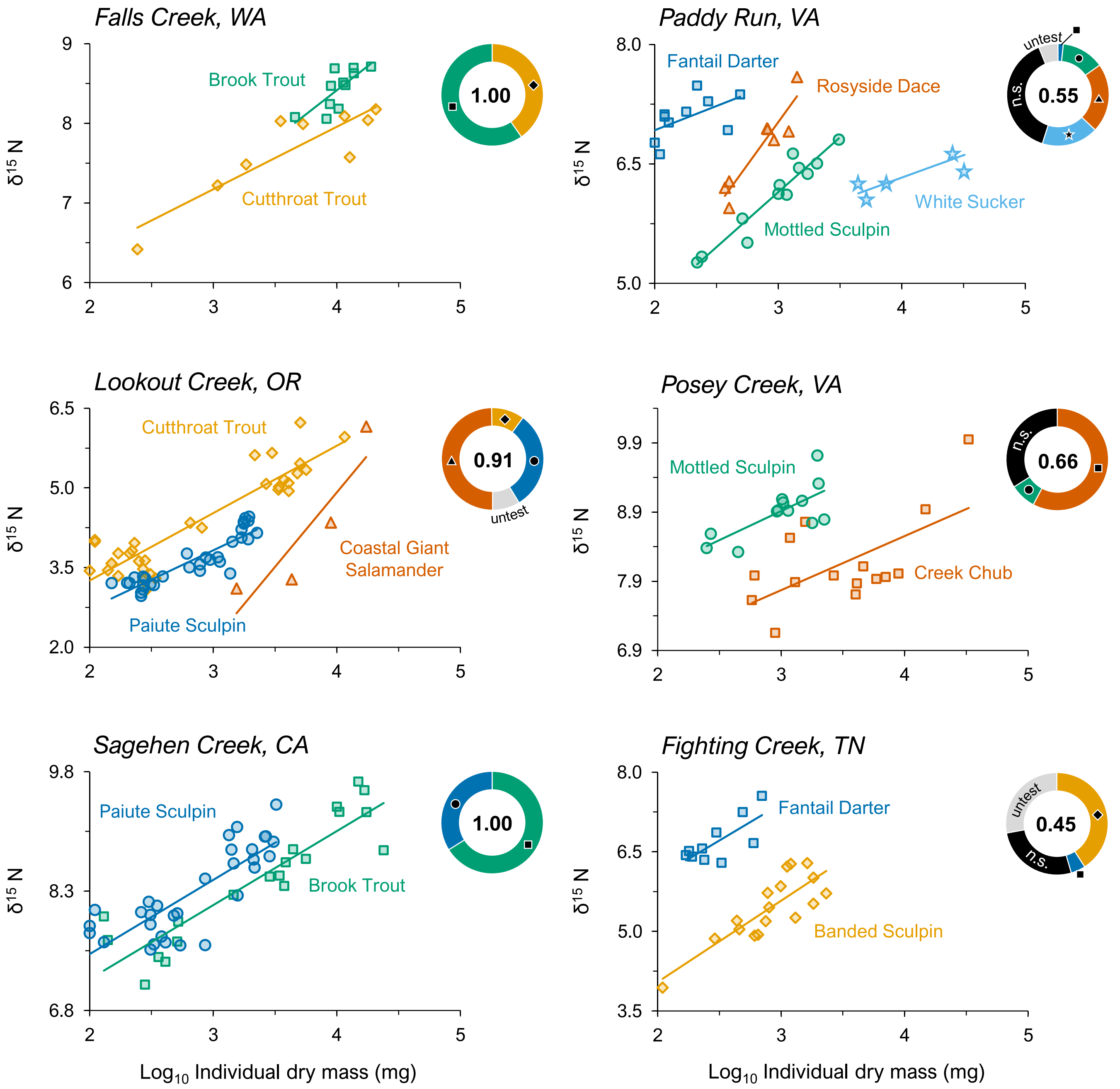

FIGURE 3 Scatterplots of individual dry mass and δ^{15}N data for vertebrates that exhibited significant *r*-STPRs, organised by study site. Each scatterplot represents multiple species, with species distinguished by colour and symbol. Coloured sections in the inset doughnut (pie) charts show the proportion of the total sample biomass in each stream that is represented by the plotted species. Black doughnut chart sections (n.s. labels) represent the cumulative biomass of species that were modelled but did not provide evidence of a significant, positive *r*-STPR. Gray sections (untest labels) represent the cumulative biomass of untested species; taxa that were collected at a given site, but not included in *r*-STPR tests due to low sample sizes ($n < 5$). The prevalence or fraction of total sample biomass comprised by species with significant *r*-STPRs is listed in the center of each doughnut chart. For instance, cutthroat trout, Paiute sculpin (*Cottus beldingii*), and coastal giant salamander (*Dicamptodon tenebrosus*), each of which exhibit a significant *r*-STPR, account for 91% of the total sample biomass in Lookout Creek

(García-Berthou, 2002; Olson, 1996; Sammons et al., 1994) are enabled by increasing mouth gape (Keppeler & Winemiller, 2020) and reinforced by selective consumption of larger prey items (Grant & Noakes, 1986; Newman & Waters, 1984; Wilbur, 1988). These changes will tend to promote positive *r*-STPRs (Arim et al., 2010), thereby creating the necessary conditions for high prevalence.

Moreover, some of the reported prevalence values may be conservative. In Lookout Creek, the *untested* fraction of standing stock biomass was comprised entirely of small, unidentified salmonids that did not meet the minimum size requirement for δ^{15}N analysis (≥100 mg dry mass). These small specimens were most likely to be juvenile cutthroat trout (*Oncorhynchus clarkii*), the dominant salmonid

TABLE 2 Summary of linear mixed-effects *r*-STPR model comparisons (likelihood ratio tests), including model degrees of freedom, *AIC* values, model deviance (dev.), χ^2 statistics with degrees of freedom, and χ^2 *p*-values. In each of the pairwise comparisons, the new model term is highlighted with bold text. The final model (bottom row) includes additive, fixed effects of individual dry mass (*DM*) and species identity and a multiplicative effect between *DM* and species, with the random effect of study site

Model	*df*	*AIC*	*dev.*	χ^2 *(df)*	χ^2 *p*
1 + (1|Site)	3	672.26	666.26		
1 + ***DM*** + (1|Site)	4	638.65	630.65	35.61 (1)	$2.41e^{-9}$
1 + *DM* + (1|Site)	4	638.65	630.65		
1 + *DM* + **Species** + (1|Site)	17	357.48	323.48	307.17 (13)	$<1.00e^{-15}$
1 + *DM* + Species + (1|Site)	17	357.48	323.48		
1 + ***DM*** **× Species** + (1|Site)	30	319.01	259.01	64.47 (13)	$8.24e^{-09}$

within the Lookout Creek drainage (Gregory & Arismendi, 2020). If so, they were constituents of the positive *r*-STPR for larger cutthroat trout in Lookout Creek and prevalence in all three western streams was effectively 1.0. Similarly, the untested group in Fighting Creek, which constituted 20% of the vertebrate biomass, included several large rainbow trout (*Oncorhynchus mykiss*) and river chub (*Nocomis micropogon*). Sample sizes were too small to model the *r*-STPR for these species, but both are size-selective predators that experience ontogenetic shifts in feeding behaviour (Bisson, 1978; Lachner, 1950; Segnini & Bastardo, 1995). Thus, it is likely that larger sample sizes would reveal positive *r*-STPRs for these two species and increase the prevalence estimate in Fighting Creek to >0.6.

Direct comparisons with other systems are not yet possible because the prevalence analyses and results are novel. However, some preliminary insight can be gained by comparing the eastern and western study streams. The observed range of prevalence values in eastern streams suggests their vertebrate communities incorporate a mix of: (1) individuals that selectively consume larger, higher trophic level prey as they grow (e.g. creek chub, *Semotilus atromaculatus*, and mottled sculpin, *Cottus bairdii*); and (2) individuals that capture prey opportunistically throughout their life histories, without evidence of size-selective or gape-limited predation (e.g. blacknose dace). This interpretation is consistent with empirical studies showing that both types of predatory behaviour are common among vertebrate taxa in small eastern streams. For instance, gut content analysis has confirmed the hypothesis of size-selective predation by creek chub (Barber & Minckley, 1971; Magnan & Fitzgerald, 1984) and mottled sculpin (Gilson & Benson, 1979; McGinley, 2013). However, gut contents studies for blacknose dace concluded that opportunistic predation is common (Bragg, 1978; Pappantoniou & Dale, 1982), with no consistent relationship between prey size and predator size (Noble, 1965).

Conspicuously absent from the eastern vertebrate samples were herbivores that selectively consume fresh photosynthetic material. For example, the central stoneroller (*Campostoma anomalum*) is a common herbivore that feeds primarily on diatoms and blue–green algae (Evans-White et al., 2001; Power & Matthews, 1983) and can achieve high densities (>2 individuals/m^2; Mundahl & Ingersoll, 1989; Power et al., 1985) when these resources are abundant. Absence of the central stoneroller within the eastern study streams, despite its known presence within the parent drainages (Etnier & Starnes, 1993; Jenkins & Burkhead, 1994; Lennon & Parker, 1960), may indicate that local instream primary production was insufficient to sustain populations of large herbivores. This hypothesis is consistent with the general observation that small, headwater streams within eastern U.S. deciduous forests are heterotrophic systems (Lamberti & Steinman, 1997; Sinsabaugh, 1997) where allochthonous litter is the predominant source of bioavailable carbon (Benfield, 1997; Hornick et al., 1981). Invertebrates with rasping mandibles can process this material (Graça, 2001; Merritt et al., 2017) but most temperate stream vertebrates lack the morphological adaptations to chew and digest refractory, allochthonous litter (Barton, 2007; Goldstein & Meador, 2004).

In the western streams, prevalence values near 1.0 suggest that all resident vertebrates are size-selective predators. This is counterintuitive because diatoms and blue–green algae are often abundant in western montane streams that receive moderate to high levels of solar radiation (Leland et al., 1986; Minshall et al., 1983; Rounick & Gregory, 1981; Zucker, 1994). In these streams, herbivorous invertebrates such as the snail *Juga silicula* and the caddisfly *Dicosmoecus gilvipes* (Ellsworth, 2000; Gard, 1961; Lamberti et al., 1995; Leland et al., 1986) are common, yet no herbivorous vertebrates were detected. This may be due to harsh environmental conditions. Steep gradients and seasonally variable flows are typical of montane streams. To persist in these systems, vertebrates must be strong swimmers with streamlined profiles. Such *rheophilic* species (Bond et al., 1988; Moyle & Cech, 2004) tend to be predatory salmonids and cottids in western streams (Beecher et al., 1988; Gard & Flittner, 1974; McGarvey & Hughes, 2008). Longitudinal barriers may also be a factor. Herbivorous vertebrates are present in the parent drainage of each of the three western streams (see next paragraph) but in each case, impassable waterfalls or dams currently prevent them from reaching the study sites.

Additional research is now needed to place the prevalence results in a broader context. I suggest two priorities as logical next steps. First, prevalence should be examined in larger, downstream reaches, then compared with the values reported here for small streams. Instream primary production rates are predicted to increase in the mid-reaches of temperate rivers, as exposure to solar radiation increases (Vannote et al., 1980). Increased biomass of primary and facultative herbivores should therefore be possible. In the eastern rivers, common herbivorous vertebrates include the stonerollers (*Campostoma sp.*), southern redbelly dace (*Chrosomus erythrogaster*; Phillips, 1969), and invasive grass carp (*Ctenopharyngodon idella*; Cudmore & Mandrak, 2004). Common western examples include the chiselmouth (*Acrocheilus alutaceus*; Lassuy, 1991), largescale sucker (*Catostomus macrocheilus*; MacPhee, 1960), and mountain sucker (*Catostomus platyrhynchus*; Hauser, 1969). As the biomass of these vertebrate herbivores increases, prevalence of positive STPRs is predicted to decrease.

Second, prevalence should be estimated for aquatic invertebrates. Predatory invertebrates are abundant in temperate streams, where they often account for *c*, 10–50% of total invertebrate biomass (Cummins & Klug, 1979; Hawkins & Sedell, 1981; Kaylor & Warren, 2017; Wallace et al., 2015). Furthermore, many invertebrate predators exhibit considerable growth throughout their life histories. For example, between the first and last instars, the widespread alderfly *Sialis californica* increases its body mass by 3 orders of magnitude (Azam & Anderson, 1969). These observations suggest that positive STPRs may exist for many aquatic invertebrates and in some cases, prevalence may be comparable with vertebrate communities.

One point of caution when interpreting the *r*-STPR and prevalence results is the variable range of body sizes among the modelled species. For example, underrepresentation of small individuals was evident for some large-bodied taxa, including coastal giant salamander, longnose dace (*Rhinichthys cataractae*) and white sucker. This may have biased the *r*-STPR model slope and intercept estimates. Similarly, variable sample sizes may have influenced some of the *r*-STPR models. For instance, low statistical power resulting from a small sample size may explain why the *r*-STPR model was significant for fantail darter (*Etheostoma flabellare*) in Paddy Run ($n = 10$) and Fighting Creek ($n = 10$), but not in Posey Creek ($n = 5$). A post hoc regression analysis revealed no significant relationship between sample size (independent variable) and the *p*-values (dependent variable) from *r*-STPR models ($F_{1,\,20} = 2.094$; $r^2 = 0.095$; $p = 0.163$). Nevertheless, larger sample sizes and complete representation of all size classes should be prioritised in future research.

Another limitation of this study was the direct use of bulk-tissue δ^{15}N data, without reference to site-specific isotopic baselines or accounting for distinct resource pools. As noted in the Methods, lack of an isotopic baseline at each site precluded estimation of absolute trophic levels and limited opportunities for comparison among systems (see Layman et al., 2012). Furthermore, multiple N source pools may have been incorporated in some of the vertebrate diets. This would bias the *r*-STPR results if the isotopic baselines of distinct pools were highly variable and species or size-classes within the same stream selectively consumed resources from different pools. In this situation, two co-occurring species or different life history stages of the same species may occupy similar trophic positions while exhibiting distinct δ^{15}N values. This scenario was implicit in the STPR meta-analysis of Riede et al. (2011), who found that positive STPRs are more often detected in lentic than lotic systems; while lakes are primarily sustained by autochthonous resources, lotic systems depend on a mix of autochthonous and allochthonous resources (Caraco & Cole, 2004). Concerns mentioned here could be addressed with mixing models that incorporate additional isotopic signatures (e.g. δ^{13}C) and appropriate baselines (Layman et al., 2012). Alternatively, the use of amino acid compound specific δ^{15}N samples, rather than bulk-tissue, would bypass the need to obtain isotopic baselines (Bowes & Thorp, 2015).

Despite these caveats, the *r*-STPR trends demonstrated in this study are comparable to STPRs reported for many other freshwater vertebrates. Examples include large piscivores such as northern pike (*Esox lucius*; Beaudoin et al., 1999; Paradis et al., 2008) and largemouth bass (*Micropterus salmoides*; Christensen & Moore, 2009; Fry et al., 1999, as well as omnivorous species, such as American gizzard shad (*Dorosoma cepedianum*; Fry et al., 1999) and bluegill sunfish (*Lepomis macrochirus*; Paterson et al., 2006). Collectively, the individual-level results reported here and elsewhere suggest that positive STPRs may be characteristic of many vertebrates in temperate freshwater ecosystems, with potential to drive moderate to high levels of prevalence. If so, it will be important to account for individual-level size-structure when studying community-level trophic dynamics.

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CONFLICT OF INTEREST

The author has no personal or financial conflict to declare.

DATA AVAILABILITY STATEMENT

All raw data are available with a R script to recreate each of the regression models on figshare (https://doi.org/10.6084/m9.figshare.12594551.v1).

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