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Use of Stable Isotopes to Test Literature-based Trophic Classifications of Small-bodied Stream Fishes

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ABSTRACT.—Defining the trophic position of stream organisms is a first step in understanding the ecology of lotic systems. Whereas trophic positions of stream fishes have been traditionally assigned based on dietary analysis, stable isotope ratios may provide additional information on the validity of this approach and may be used to verify energy acquisition assumed from dietary studies. In this study, we assessed the concordance of literature-based trophic classifications and isotopic $\delta^{15}\text{N}$ signatures for small-bodied fishes from four streams in Kansas, Oklahoma and New Mexico. ANOVA results revealed no significant difference ($F_{2,27} = 1.71$, $P = 0.201$) in trophic position based on $\delta^{15}\text{N}$ values among three broad trophic classifications derived from literature sources (algivores/detritivores, omnivores and invertivores). Both the prevalence of omnivory in stream fishes and potential biases associated with isotope fractionation at different trophic levels poses potential problems when classifying lotic fish into trophic positions.

INTRODUCTION

Trophic classification of fishes aids our understanding of interactions among aquatic organisms by providing a general index of diet overlap and a basis for the construction of food webs. This information can be used to make inferences on the direct or indirect influences of species within or among trophic groups. Trophic groupings also provide insight into the functional roles (*e.g.*, top down versus bottom up effects) that fishes play in aquatic systems (Power, 1992; Gelwick *et al.*, 1997; Matthews, 1998). Understanding these food web interactions is often necessary for conservation. For example, resource use by introduced species might help predict which species are successful invaders as well as their potential effects on native fish assemblages (Moyle and Light, 1996; Kolar and Lodge, 2002). Moreover, trophic classification is central to indices of biotic integrity that are commonly used to evaluate stream health (Karr, 1981). Given the overwhelming importance of trophic classification in the field of aquatic ecology, it is necessary to evaluate classification schemes across species and aquatic habitats.

Two common methods for classifying fishes into trophic groups are diet and stable isotope analysis. Diet analysis, based on an evaluation of ingested material, only reflects recently consumed items (<24 h), and does not discriminate between ingested and assimilated

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material. Gut contents might indicate the structural affects of fishes in ecosystems, as most materials ingested (assimilated or not) are killed or at least temporarily removed from the system. More recently, the ratio of ^{15}N : ^{14}N has been used as an indicator of trophic position and the ratio of ^{13}C : ^{12}C as an indicator of carbon source. Stable isotope ratios differ from traditional gut content analysis by providing a time-integrated measure of trophic position that only reflects items that were assimilated by the organism. However, the use of isotopes is limited by system specific variability in baseline isotope ratios (Vander Zanden *et al.*, 1997; Vander Zanden and Rasmussen, 1999) and trophic shifts may not immediately be reflected in the isotopic signatures of fishes due to tissue turnover time lags, which are dependant on growth rates and the metabolic rates of specific tissues (Hesslein *et al.*, 1993; Sakano *et al.*, 2005). Assuming these biases are controlled, differences between diet and stable isotope analysis should reflect differential assimilation of ingested material.

Our primary objective was to use the N isotope signature of muscle tissues to test trophic classifications of small-bodied stream fishes based on literature-based diets. Whereas isotopic ratios of N should be notably different among trophic specialists from different trophic levels, classifying omnivorous fishes into trophic positions may be problematic (Gu *et al.*, 1997; Pinnegar and Polunin, 2000; Ponsard and Arditì, 2001; Jepsen and Winemiller, 2002). Because our focal river systems are often characterized by highly variable environmental conditions, opportunistic fishes that feed at more than one trophic level and that can withstand fluctuating environmental conditions are expected to persist in these environments (Winemiller and Rose, 1992; Rabeni, 1996; Dodds *et al.*, 2004). Thus, we predicted a weak relationship between N isotope ratios and a trophic classification based on literature sources that primarily relied on diet analysis.

METHODS

Study area.—Fish assemblages and chironomids were sampled from four streams to evaluate the relationship between diet and stable isotope signature of fishes. Wildcat Creek, Kansas, is a medium-sized stream having a mean discharge of $0.06 \text{ m}^3 \text{ s}^{-1}$ with moderate increases in discharge during spring. The catchment encompasses approximately 190 km^2 and the stream substrate is comprised of limestone bedrock and large cobbles. Catchment area of the Kansas and Canadian River basins are $117,171 \text{ km}^2$ and $49,210 \text{ km}^2$ and mean discharge is $166 \text{ m}^3 \text{ s}^{-1}$ and $174 \text{ m}^3 \text{ s}^{-1}$, respectively. Flows are seasonally quite variable and substrates are dominated by shifting sand. The San Juan River, New Mexico drains $99,200 \text{ km}^2$ in southwestern Colorado and northwestern New Mexico (Carlson and Carlson, 1982). Mean discharge is $68 \text{ m}^3 \text{ s}^{-1}$ and regularly peaks in the Spring during snow melt. Substrate is predominantly sand and cobble.

Sampling methods.—Fishes and chironomids were collected from Wildcat Creek in October 2002, the Kansas River in October 2003, the Canadian River in March 2003, and the San Juan River in July 2003. All fishes were collected with a $4.6 \text{ m} \times 1.2 \text{ m}$ (3.2-mm mesh) seine and chironomids were sifted from fine sediments with a $250 \text{ }\mu\text{m}$ sieve. All samples collected were frozen on site in dry ice. Each site was sampled intensively for approximately 1 h or until no new fish species were encountered. We focused our analysis on species with widespread distributions across sites; including species native to the Kansas and Oklahoma rivers and introduced into the San Juan River (*e.g.*, *Cyprinella lutrensis*, *Gambusia affinis*, *Ictalurus punctatus* and *Pimephales promelas*). However, we also analyzed some species that were unique to particular river systems (*e.g.*, *Etheostoma spectabile* and *Hybognathus placitus*).

Fishes examined from streams in the Mississippi River basin were native to this system, but *Pimephales vigilax* and *G. affinis* have been transferred from the Arkansas River to the Kansas River and Wildcat Creek. All fishes used for stable isotope and diet analysis were <100 mm standard length.

Stable isotope method.—Dorsal muscle tissue was taken from a minimum of three individuals from each fish species for stable isotope analysis. The use of white muscle tissue for stable isotope analysis has lower variability in $\delta^{15}\text{N}$ compared to other tissues, and does not require acidification to remove inorganic carbonates (Pinnegar and Polunin, 1999). Samples were dried at a constant temperature (60 C) for 48 h before grinding into powder with a mortar and pestle. Samples (≈ 2.5 mg) were analyzed for $\delta^{15}\text{N}$ in the Stable Isotope Mass Spectrometry Laboratory (SIMSL), at Kansas State University with a ThermoFinnigan Delta Plus mass spectrometer with a CE 1110 elemental analyzer and ConFlo II interface in continuous flow mode (CF-IRMS). Stable isotope ratios were calculated in the standard notation:

$$\delta^{15}\text{N} = \left[\frac{{}^{15}\text{N}/{}^{14}\text{N}_{\text{sample}}}{{}^{15}\text{N}/{}^{14}\text{N}_{\text{standard}}} \right] - 1 \times 1000$$

Values are expressed on a per mil (‰) basis. Overall, there was little variability within species taken from the same collection site in $\delta^{15}\text{N}$; mean coefficient of variation (cv) = 6.6% \pm 3.1% SD.

Trophic classification by literature.—We compiled literature descriptions of diet for the species used in our analysis from regional species accounts (Table 1). To simplify analyses, species were classified into one of three groups: algae/detritivore, omnivore or invertivore. If diet descriptions included both invertebrates and algae or detritus, they were classified as omnivores. Most diet descriptions represented adults; however, additional sources were used for juvenile *Micropterus salmoides*, *Catostomus latipinnis*, *Carpiodes carpio* and *Ictalurus punctatus* because $\delta^{15}\text{N}$ values only were obtained from juveniles of these species. If literature sources differed in their classification of a species, we selected the classification that was used in the majority of cases.

Diet analysis method.—In addition to trophic classification based on our literature review, we characterized diet from the individuals used for isotopic analysis. Diet was based on the contents in the upper portion of the gut to the first bend in the digestive tract (Bowen, 1996). Contents were spread on a 0.8 mm grid in a petri dish, and percent area for each food item was recorded. The area each diet item occupied was assumed to be proportional to its volume (Hellowell and Abel, 1971). The mean percent area occupied by each diet item was calculated for each fish species in all systems. Although gut contents were identified to the lowest possible taxonomic group, diet items were placed into two categories (invertebrates, algae/detritus) to be consistent across sites. Therefore, diet data represented a coarse evaluation of food habits that was used to classify species as invertivores, omnivores or algivore/detritivores. Trophic positions were inferred from the mean percent area of food items in the gut; omnivores were classified as having on average >25% of invertebrates and algae/detritus, invertivores having >75% invertebrates and algivore/detritivores having >75% algae/detritus in their gut (Adams and Kimmel, 1983).

Hereafter, we refer to the three different methods used to assign trophic position as (TP_{lit}) for literature classification, (TP_{diet}) for our diet classification, and (TP_{si}) for stable isotope classification.

Data analysis.—We tested for differences in $\delta^{15}\text{N}$ among TP_{lit} classifications using ANOVA. Because consumers are consistently $\delta^{15}\text{N}$ enriched ($3.4 \pm 0.3\text{‰}$) compared to their prey (Cabana and Rasmussen, 1994), we predicted that the highest trophic level based on TP_{lit}

TABLE 1.—Species code, number of guts analyzed, specific and average literature trophic classification (TP_{lit}), our trophic classification based on diet (TP_{diet}), percent invertebrates found in the diet and trophic position based on $\delta^{15}\text{N}$ values (TP_s) from stream fishes sampled from four systems

Species	Species code	Number of guts analyzed	Cross and Collins (1995)	Smith (1979)	Robison and Buchanan (1984)	Sublette <i>et al.</i> (1990)	Pfeiger (1997)	Ross (2001)	Miller and Robison (2004)	TP _{lit}	TP _{diet}	Percent inverts in diet	TP _s
<i>Campostoma anomadum</i>	CAMANO	5	ALG	—	ALG	ALG	ALG	ALG	ALG	ALG	ALG	0	2.85
<i>Cyprinella lutrensis</i>	CYPLUT	94	OMN	INV	OMN	OMN	OMN	OMN	OMN	OMN	OMN	49	2.79
<i>Cyprinus carpio</i>	CYPCAR	8	OMN	OMN	OMN	OMN	OMN	OMN	OMN	OMN	OMN	64	3.28
<i>Hypognathus placitus</i>	HYBPLA	9	ALG	—	ALG	ALG	ALG	—	ALG	ALG	ALG	0	2.71
<i>Lythrurus umbratilis</i>	LYTUMB	9	INV	—	OMN	—	INV	OMN	OMN	OMN	OMN	67	3.01
<i>Notropis atherinoides</i>	NOTATH	18	INV	OMN	OMN	—	OMN	OMN	INV	OMN	OMN	31	3.46
<i>Notropis stramineus</i>	NOTSTR	18	INV	OMN	OMN	OMN	OMN	—	OMN	OMN	INV	80	3.45
<i>Rhinichthys osculus</i>	RHIOSC	43	—	—	—	INV	—	—	—	INV	INV	96	3.45
<i>Pimephales notatus</i>	PIMNOT	5	OMN	OMN	OMN	—	OMN	OMN	OMN	OMN	ALG	0	3.41
<i>Pimephales promelas</i>	PIMPRO	20	OMN	OMN	OMN	OMN	OMN	OMN	OMN	OMN	OMN	25	3.13
<i>Pimephales vigilax</i>	PIMVIG	39	INV	—	OMN	OMN	OMN	INV	OMN	OMN	OMN	40	3.19
<i>Semotilus atromaculatus</i>	SEMATR	6	INV	OMN	INV	—	INV	INV	INV	INV	INV	73	3.01
<i>Carpiodes carpio</i>	CARCAR	7	OMN	OMN	OMN	OMN	OMN	OMN	OMN	OMN	ALG	0	3.21
<i>Catostomus discobolus</i>	CATDIS	n/a	—	—	—	ALG	—	—	—	ALG	—	n/a	3.21
<i>Catostomus latipinnis</i>	CATLAT	33	—	—	—	OMN	—	—	—	OMN	OMN	58	3.20
<i>Ictalurus punctatus</i>	ICTPUN	30	INV	OMN	INV	INV	INV	OMN	OMN	INV	INV	84	3.30
<i>Noturus exilis</i>	NOTEXI	8	INV	INV	INV	—	INV	INV	INV	INV	INV	77	3.26
<i>Gambusia affinis</i>	GAMAFF	29	INV	INV	OMN	INV	OMN	OMN	INV	INV	INV	60	2.96
<i>Lepomis humilis</i>	LEPHUM	41	INV	—	INV	—	INV	INV	—	INV	INV	94	3.09
<i>Micropterus salmoides</i>	MICSAL	9	INV	INV	INV/PIS	PIS	INV	INV	INV	INV	INV	100	3.38
<i>Etheostoma spectabile</i>	ETHSPE	8	INV	INV	INV	—	INV	—	INV	INV	INV	100	3.61

TABLE 2.—Species richness, number of species analyzed and range of $\delta^{15}\text{N}$ values of fishes analyzed for $\delta^{15}\text{N}$ in each stream system. $\delta^{15}\text{N}$ values for chironomidae are given as a baseline for each system

Stream system	Richness	Species analyzed	Range of $\delta^{15}\text{N}$	Chironomidae $\delta^{15}\text{N}$
Wildcat Creek	13	10	10.78 to 13.53	8.05
Kansas River	11	5	15.60 to 18.13	11.50
Canadian River	11	6	12.61 to 15.17	10.20
San Juan River	9	8	12.24 to 13.65	8.90

would also be $\delta^{15}\text{N}$ enriched. Basal trophic levels may vary temporally in $\delta^{15}\text{N}$ among sites (Velinsky *et al.*, 1989; Paerl and Vogel, 1994), therefore the TP_{si} of fishes was calculated relative to a primary consumer (*i.e.*, chironomids) in each system (Cabana and Rasmussen, 1996) with the formula:

$$\text{TP}_{\text{si}} = [(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{chironomids}})/3.4] + 2$$

The use of long-lived primary consumers (*e.g.*, mussels) as a basal trophic level accounts for temporal system variation of $\delta^{15}\text{N}$; however, no long-lived invertebrates were abundant enough at all study sites. Rather, chironomidae, which have relatively short life cycles, were used. Although chironomids may display temporal variation in $\delta^{15}\text{N}$ that is not reflected in secondary consumers, a comparison of $\delta^{15}\text{N}$ with grazing Ephemeroptera spp. from three of the four sites revealed only minor differences (0.03–0.07 $\delta^{15}\text{N}$).

We assessed the relationship between percent invertebrates found in the diet and TP_{si} using Pearson's product moment correlation. We hypothesized higher invertebrate content in the diet will result in an increase in TP_{si} .

RESULTS

The number of species collected at the four study sites varied from 9 to 13, but diet and isotope analysis was only performed on 6 to 10 common species from each site (Table 2). Species that were represented by <5 individuals with non-empty stomachs were not included in the analysis. These species included: *Noturus flavus* in Wildcat Creek, *N. atherinoides* in the Kansas River and *Ictalurus punctatus* in the Canadian River. By excluding these rare species, we described the trophic positions of the most abundant taxa in each river system.

Diet studies suggested that fishes analyzed from the four systems fed from one or two trophic levels; algae/detritus and invertebrates. The TP_{lit} classifications were not consistent for all species, primarily omnivores. Our classification of TP_{diet} matched TP_{lit} for most species. However, we placed *Pimephales notatus*, *Gambusia affinis* and *Carpiodes carpio* at lower trophic levels and *Notropis stramineus* at a higher trophic level (Table 1). Our diet classifications were also somewhat consistent with TP_{si} , in that the percent invertebrates in the diet and TP_{si} showed a positive, but weak correlation ($r = 0.42$, $P = 0.06$; Fig. 1).

The range of $\delta^{15}\text{N}$ values among species in each system was greatest in Wildcat Creek (2.75 $\delta^{15}\text{N}$) and least in the San Juan River (1.41 $\delta^{15}\text{N}$) (Table 2). Unfortunately, tests for differences in TP_{si} among groups based on TP_{lit} could not be conducted at each site because we lacked replication in the algivore/detritivore trophic group at all sites, and invertivores in the Canadian and Kansas rivers (Fig. 2). Across all systems, there was no significant difference in TP_{si} among algivore/detritivores, omnivores and invertivores ($F_{2,27} = 1.71$, $P = 0.201$; Fig. 3). This was likely because of the large variation in TP_{si} within these three trophic groups, in particular omnivores.

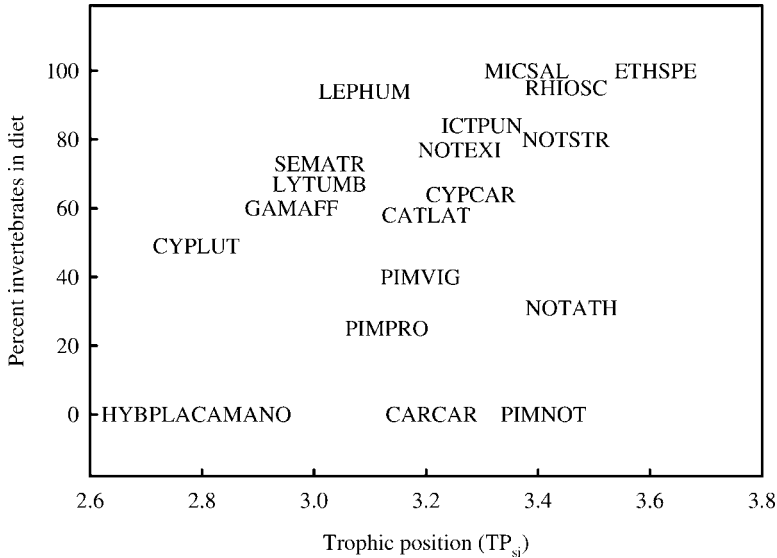


FIG. 1.—Relationship between percent invertebrates in the diet and trophic position based on $\delta^{15}\text{N}$ (TP_{si}) from all systems ($r = 0.42$, $P = 0.06$). Fishes are represented by their species code explained in Table 1

DISCUSSION

Our results contrast a number of studies in aquatic systems that report clear differences in stable isotope signatures among trophic groups (Vander Zanden *et al.*, 1997; Beaudoin *et al.*, 1999; Fisher *et al.*, 2001; Grey, 2001; Guiguer *et al.*, 2002; Renones *et al.*, 2002; Manetta *et al.*, 2003). However, most of these studies were from lentic systems that typically had longer food chains ($\geq 3^\circ$ consumers) and more distinct trophic groups (*i.e.*, less omnivory). Fishes analyzed in our study only fed from two trophic levels, and many species were classified as omnivores. This weak association between TP_{lit} and TP_{si} is consistent with results from other systems that are dominated by omnivores (Gu *et al.*, 1997; Pinnegar and Polunin, 2000; Jepsen and Winemiller, 2002).

The literature classification (TP_{lit}) accurately reflected trophic positions based on stable isotopes (TP_{si}) for some species (*e.g.*, *Etheostoma spectabile*, *Campostoma anomalum*) but not others (*e.g.*, *Catostomus discobolus*, *P. notatus*). This lack of a general concordance across groups may be attributed to more variable fractionation of $\delta^{15}\text{N}$ in herbivores than carnivores (Vander Zanden and Rasmussen, 2001; McCutchan *et al.*, 2003). Three putative primary consumers were represented in the analysis, *C. anomalum*, *C. discobolus* and *Hybognathus placitus*. *Campostoma anomalum* and *H. placitus* both occupied low TP_{si} , as expected based on TP_{lit} ; however, *C. discobolus* held a higher TP_{si} than expected. *Catostomus discobolus* could be either assimilating more energy from higher trophic levels than expected from its diet, or have higher isotopic fractionation than other herbivores in our analysis.

Differential assimilation of diet items also might reduce the resolution of TP_{si} , particularly for omnivores that might assimilate invertebrates more readily than algae or detritus (Jepsen and Winemiller, 2002). For example, TP_{lit} of *Pimephales notatus* suggests they are omnivores, but TP_{diet} suggests they are algivore/detritivores. Although TP_{diet} was only based

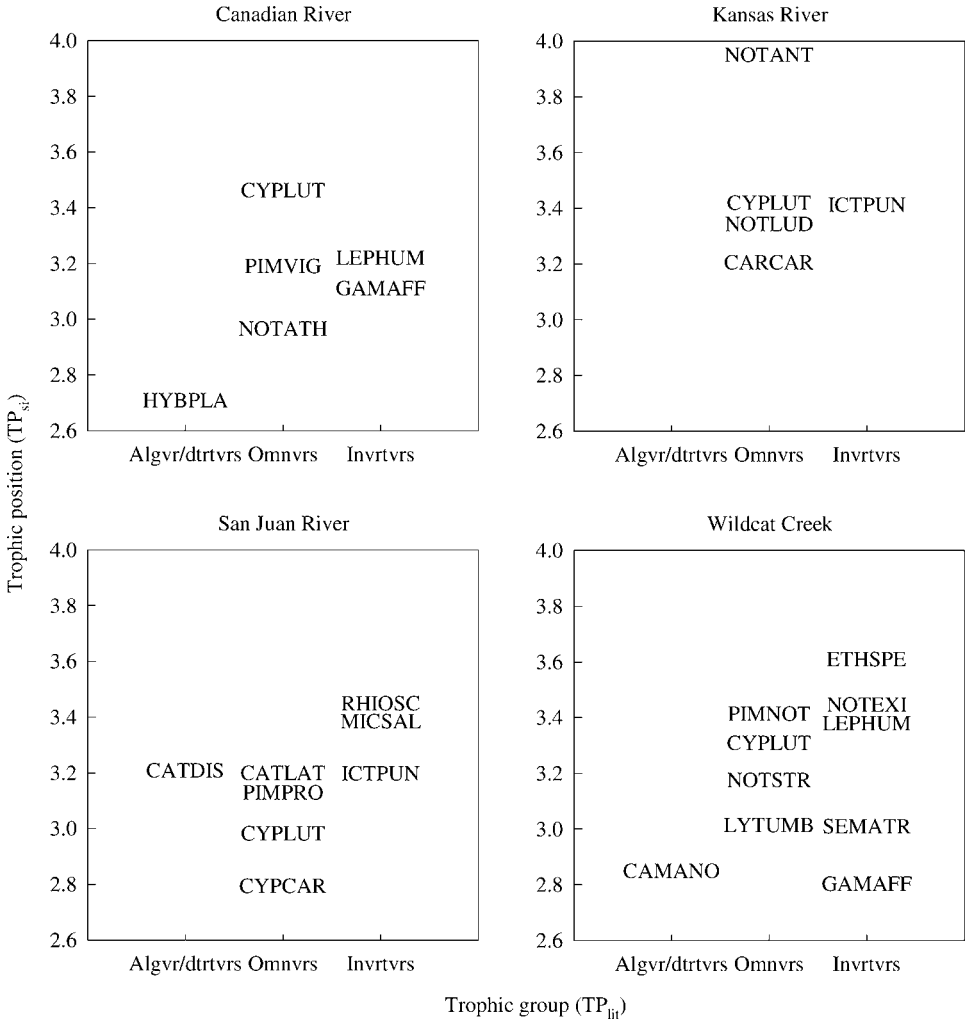


FIG. 2.—Mean trophic position of fishes based on $\delta^{15}\text{N}$ (TP_{si}) and trophic groups based on diet reported in previous literature (TP_{ii}), for each study stream. Fishes are represented by their species code explained in Table 1

on a snapshot of this species diet, diets of numerous other specimens have confirmed their basal feeding habit from this area (Gido *et al.*, unpubl. data) and elsewhere (Whitaker, 1977). Nevertheless, TP_{ii} provided the best match with TP_{si} in Wildcat Creek, suggesting that *P. notatus* might obtain a considerable amount of energy from a higher trophic level than their diet suggests.

Omnivorous fishes can demonstrate substantial variability in feeding ecology across sites (Gu *et al.*, 1997) attributed to spatial and temporal variability in lotic systems. The stochastic hydrology in large rivers in this region selects for the prevalence of opportunistic feeding strategies (Fausch and Bestgen, 1997). Given the dietary shifts and temporal and spatial

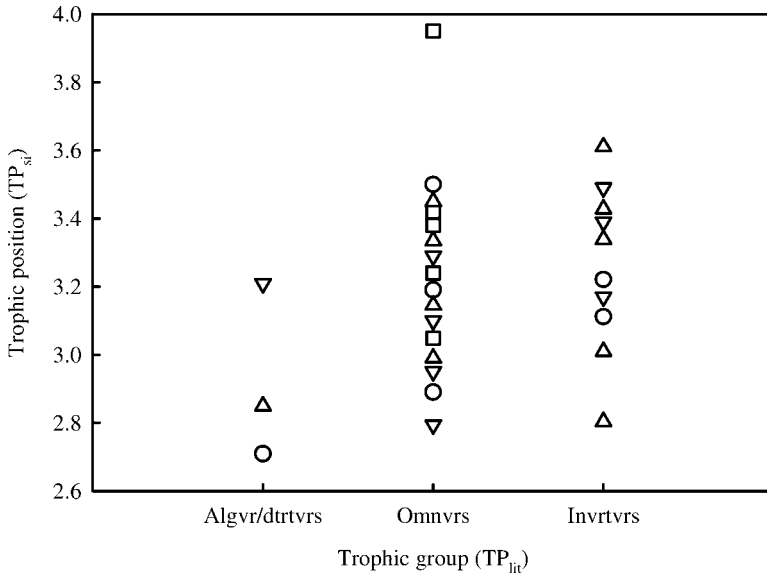


FIG. 3.—Mean trophic position of fishes (TP_{si}) from different trophic groups based on diet reported in previous literature (TP_{lit}), across all streams. Fishes are represented by ▽—San Juan River, ○—Canadian River, □—Kansas River and △—Wildcat Creek

variation in feeding ecology of these fishes, it is difficult to accurately quantify trophic position based solely on diet analysis. The use of stable isotopes might be a better tool for quantifying the average trophic position a fish occupies through its lifetime whereas diet analysis provides an index of consumption. The ideal approach would include both diet and stable isotope analyses to elucidate both the trophic positions and functional roles of prairie stream fishes.

The use of indices such as the index of biotic integrity in prairie rivers (IBI; Bramblett and Fausch, 1991; Bramblett *et al.*, 2005) relies on accurate descriptions of life history traits to evaluate the condition of stream ecosystems. However, based on the results of this study, it is important to use caution when basing trophic classification based only on literature reports and a lack of concordance among literature sources may leave managers with conflicting estimations of trophic positions. Therefore, a consensus of isotope and diet data may help resolve the trophic positions of problematic species and provide a better understanding of the dynamic feeding ecology of prairie stream fishes.

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