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Letter

Comparing trophic position of stream fishes using stable isotope and gut contents analyses

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Abstract – Stable isotope analysis (SIA) and gut contents analysis (GCA) are commonly used in food web studies, but few studies analyse these data in concert. We used SIA (δ^{15}N) and GCA (% composition) to identify diets and trophic position (TP) of six stream fishes and to compare TP estimates between methods. Ordination analysis of gut contents identified two primary trophic groups, omnivores and predators. Significant differences in TP_{GCA} and TP_{SIA} were similar in direction among-species and among-trophic groups; neither method detected seasonal changes in omnivore diets. Within-species TP_{GCA} and TP_{SIA} were similar except for one omnivore. TP_{GCA} was less variable than TP_{SIA} for predators, but variation between methods was similar for omnivores. While both methods were equally robust at discriminating trophic groups of fishes, TP_{SIA} is less laborious to estimate and may facilitate cross-stream comparisons of food web structure and energy flow.

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Introduction

The food web model is an effective tool for describing trophic relationships among organisms (Woodward & Hildrew 2002), tracking the flow of organic matter within a community (Rosi-Marshall & Wallace 2002), and predicting contaminant levels within and among populations (Cabana & Rasmussen 1994; Vander Zanden & Rasmussen 1996). Grouping organisms by trophic level (i.e., producer = 1, herbivore = 2, predator = 3) loosely characterises their relative position within a food web, but this categorical approach does not account for complex trophic interactions such as omnivory (Kling et al. 1992). Trophic position (TP) is a continuous variable that accounts for omnivory and better quantifies matter and energy flow within a food web (Kling et al. 1992; Vander Zanden & Rasmussen 1996; Post 2002). Traditionally TP has been calculated from gut contents analysis (GCA). GCA also provides detailed information on species' diets, but does not account for long-term patterns of mass transfer and provides only an instantaneous measure of an organism's diet (Vander Zanden et al. 1997). Additionally, GCA is laborious and requires considerable taxonomic expertise, especially when investigating the diets of insectivorous fishes.

Stable isotope analysis (SIA) is increasingly being used to calculate TP in aquatic systems (e.g., Post 2002; Jardine et al. 2006). SIA is an effective means of tracking matter and energy flow through communities (Peterson & Fry 1987; Kling et al. 1992; Cabana & Rasmussen 1996; Vander Zanden & Rasmussen 1996). The isotopic ratio of nitrogen ($^{15}N/^{14}N$), henceforth referred to as δ^{15}N, has successfully identified trophic relationships in aquatic food web studies (Peterson & Fry 1987). Organisms preferentially sequester ^{15}N through isotopic fractionation and subsequently become enriched by about 3.4‰ compared to their prey, although a wide range of fractionation rates have been observed (Post 2002; McCutchan et al. 2003). Determining an organism's TP from its δ^{15}N signature is possible by adjusting for baseline δ^{15}N signature of the environment although this does not correct for variation in the fractionation rate among fishes (Cabana & Rasmussen 1996). As δ^{15}N of basal resources (e.g., periphyton, detritus, etc.) is prone to high temporal variability, a primary consumer is commonly used to calculate baseline correction factors (Cabana & Rasmussen 1996).

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Although $\delta^{15}N$ is useful for establishing trophic relationships within foodwebs, it cannot provide direct evidence of an organisms prey items (i.e., specific invertebrate taxa).

To provide a robust characterisation of mass and energy transfer within a food web, SIA should be used in conjunction with GCA (Vander Zanden et al. 1997; Woodward & Hildrew 2002). Using GCA and SIA in concert can provide a thorough characterisation of an organism's feeding habits (e.g., identity, number, and size of prey items) and TP (Renones et al. 2002). Combined use of GCA and SIA has been successful in constructing food web models in many aquatic systems; however, few researchers have directly compared results from both analyses (e.g., Creach et al. 1997; Whitledge & Rabeni 1997; Jones & Waldron 2003). Vander Zanden et al. (1997) demonstrated that GCA and SIA provide comparable estimates of fish TP in lake ecosystems. However, few studies have calculated TP of stream fishes, and direct comparisons between the two methods in stream ecosystems are generally lacking (but see Franssen & Gido 2006). Our study had three objectives. First, we identified seasonal and among-species variation in diet of six species of stream fishes using GCA. Literature descriptions of fish diets indicated that these species are either invertivorous (henceforth, predators) or omnivorous, and we expected to find similar patterns at our sites. Second, we calculated TP for these fishes based on GCA and SIA and evaluated the ability of the two methods to differentiate seasonal, among species, and among trophic group differences in diet. Finally, we compared TP_{GCA} and TP_{SIA} to determine if they yielded similar results.

Methods

Study sites and fishes

Twelvemile Creek is located near Clemson, South Carolina in the southeastern USA and flows into Lake Hartwell, a reservoir on the Savannah River. Most of the drainage basin lies within the Piedmont physiographic province, with some headwaters in the Blue Ridge. Four sampling sites were established along Twelvemile Creek, as well as two sites on Town Creek, a tributary of Twelvemile Creek. The longitudinal distance between the upstream- and downstream-most sites was 24 stream km. Detailed site geomorphology and locality data are provided in Walters et al. (2007).

Fishes were selected based on ubiquity and feeding guild (predators and omnivores) to facilitate comparison of GCA and SIA data over a gradient of fish TP. Predators included blackbanded darter (*Percina nigrofasciata*, Mathur 1973), turquoise darter (*Etheostoma inscriptum*, Baker 2002), and northern hogsucker (*Hypentelium nigricans*, Matheny & Rabeni 1995). Omnivores included yellowfin shiner (*Notropis lutipinnis*, Reisen 1972) and bluehead chub (*Nocomis leptocephalus*, Jenkins & Burkhead 1994). Rosyface chub (*Hybopsis rubrifrons*) was included in the study, but diet information for this species is generally lacking in the literature.

Sample collection

Sampling was conducted in May (spring) and November (autumn) of both 2003 and 2004. Four sites were sampled in both spring and autumn and two sites were sampled only in spring. Methods for field collection of macroinvertebrates and fishes and treatment of tissues for stable isotopes analysis are detailed in Walters et al. (2007). Three replicate composite SIA samples were collected for each species at each sampling event whenever possible. Within-population variance of consumers was minimised by compositing tissue from three individuals in replicate samples whenever possible (Lancaster & Waldron 2001). To avoid potentially confounding effects of ontogenetic variation in diet on isotopic values, we preferentially selected adult fish of similar size (i.e., <10% variation in length) for inclusion in a replicate. Likewise, individual macroinvertebrates of a similar size or cohort were included in composite samples. Whenever possible, 20 individuals of each species were collected at each sampling event (season/site), although actual sample sizes ranged from 2 to 20. Fish sampling was generally conducted mid-morning to minimise the effects of diel variability in feeding patterns.

Gut contents analysis

Fishes collected for GCA were preserved in formalin. Preserved fishes were exenterated and the entire viscera placed in 70% ethanol. Each stomach was dissected and the contents removed manually with the aid of a dissecting microscope at 10× magnification. As cyprinids and catostomids lack true stomachs, the gut section from the oesophagus to the first 180° bend was used. Diets were quantified using a combination of modified volumetric (Hellawell & Abel 1971) and 'points methods' (Hynes 1950). Volumetric analysis was conducted on all dietary items except for a mixture of inseparable, homogeneously sized, microscopic items such as algal cells and amorphous detritus that were prevalent in omnivore guts. A modified version of Hynes' points method where proportions of microscopic items were visually estimated by area, was used to quantify this fraction of fish diet. This method was chosen over other methods of GCA

(Hyslop 1980) due to the inseparable nature of the microscopic fraction.

Stomach contents were transferred to a depression slide and squashed to 1-mm depth. The total area of the contents was measured with Image-Pro (Media Cybernetics, Silver Spring, MD, USA) digitising software. Area was multiplied by depth of the depression slide to determine total volume of the stomach contents. Contents were then divided into (i) readily identifiable invertebrates and (ii) 'ooze' – an inseparable mixture of amorphous detritus, algal cells, and highly macerated invertebrates and plant matter (Whitaker 1977). The relative proportion of each food type (i.e., aquatic plant matter, amorphous detritus, etc.) contributing to the total volume of ooze was estimated by area. Proportions were visually estimated and recorded for 10 haphazardly chosen quadrants using a depression slide with a 1-mm^2 grid and compound microscope at 100×. The proportion of each food type was then calculated as a percent of the total volume of ooze. The volume of each of these two fractions (invertebrates and ooze) was determined as described for total volume.

Dietary items were divided into nine food categories; aquatic, terrestrial, and unknown invertebrates, aquatic, terrestrial, and unknown plant matter, amorphous detritus (henceforth, detritus), fish/fish eggs, and inorganic material. Inorganic material was excluded from further analyses. Invertebrates were identified, and the proportion of each taxon to the total volume of invertebrates was determined by area using a 1-mm^2 grid.

Stable isotopes analysis

Samples were prepared for isotopic analysis by freeze drying and then grinding to a fine powder using a ball mill. Samples were combusted to N_2 and analysed in a Carlo Erba NA 1500 CHN analyser (Carlo Erba Instrumentazione, Milan, Italy) connected to a Finnigan Delta C isotope ratio mass spectrometer (Thermo Electron, Waltham, MA, USA) to determine $\delta^{15}N$. Reference standard for $\delta^{15}N$ was atmospheric N_2. Reproducibility was monitored using bovine liver (National Institute of Standards and Technology #1577b), and precision was <0.2‰ (1 SD).

Statistical analysis

Nonmetric multidimensional scaling (NMS) was used to identify among-species and temporal variation in diet. This procedure was chosen over other ordination techniques because of its applicability to non-normal ecological datasets (McCune & Grace 2002). Mean proportional gut composition data for each species, season, and site were arc-sine, square root transformed prior to analysis. NMS analysis was performed using PC-ORD 4.0 (MjM Software Design, Gleneden Beach, OR, USA) according to the suggested procedure of McCune & Grace (2002). All terrestrial insects and arachnids were combined into a single category, terrestrial invertebrate. Adult and larval Elmidae were combined into a single category because both life stages are fully aquatic and have similar trophic habits (Merritt & Cummins 1996). Multiple response permutation procedure (MRPP), a nonparametric procedure for testing differences between groups (McCune & Grace 2002), was used to test the hypothesis that the diets of feeding guilds were different and that diet within guilds varied by season. The MRPP test was conducted on the ranked transformed Bray–Curtis (Sorenson) distance matrix (McCune & Grace 2002) using PC-ORD 4.0.

Gut contents analysis derived TP of fishes (TP_{GCA}) was calculated according to the methods of Vander Zanden et al. (1997) using the equation:

$$TP_{GCA} = \sum (P_i * T_i) + 1$$

for each species at every sampling event (season/site), where P_i is proportion of the ith food item and T_i is TP of each food item. TP of food items was based on literature dietary data (Merritt & Cummins 1996; Vander Zanden et al. 1997). For example, predatory insects were assigned a TP of 3.0, omnivorous invertebrates were assigned a TP of 2.5, herbivorous invertebrates were assigned a TP of 2.0, and plant material was assigned a TP of 1.0.

Stable isotope analysis derived TP of fishes (TP_{SIA}) was calculated according to the methods of Cabana & Rasmussen (1996) using the equation:

$$TP_{SIA} = [(\text{fish } \delta^{15}N - \text{primary consumer } \delta^{15}N)/3.4] + 2$$

for each species at every sampling event (season and site). Primary consumer $\delta^{15}N$ was calculated as the mean $\delta^{15}N$ of all primary consumers (i.e., filter feeder, collector gatherer, shredder and grazer taxa) collected for a sampling event. We pooled $\delta^{15}N$ among primary consumers to make baseline corrections because a suitable ubiquitous and abundant taxon was lacking. Trophic guilds were assigned using life history information in Merritt & Cummins (1996), and a complete taxa list including guild assignments is in Walters et al. (2007).

Two-factor analysis of variance (ANOVA) was used to test for differences in both TP_{GCA} and TP_{SIA} among species and seasons. No TP_{GCA} data were available for spring 2003 due to a catastrophic laboratory event, so; this sampling date was excluded from analysis. Sites were pooled for each species and season to allow

testing for differences among factors. To test for differences in TP_{SIA} among species and seasons, ANOVA (2-factor) was also used. Replicate samples from each sampling event were averaged, and then sites were pooled for each species and season as previously described for TP_{GCA}. Data from all seasons were included in this analysis; however, replicate stable isotope samples from spring 2004 were mistakenly pooled prior to analysis and as a result $N = 1$ for that season.

Estimated TP_{SIA} and TP_{GCA} were compared within each species using Student's *t*-test. Average TP for each site and season within each species were used in this analysis. Only data from sampling efforts that yielded both TP_{SIA} and TP_{GCA} were included. Coefficient of variation (CV) was also calculated to compare variance of TP estimates (GCA and SIA) between trophic groups.

Results

Gut contents analysis

We identified gut contents of 702 fishes, of which 130 individuals were empty and excluded from analysis (see Supplementary Material, Appendix S1). Blackbanded darter, turquoise darter, and northern hogsucker consumed mostly aquatic invertebrates (Fig. 1, see also Supplementary Material, Appendix S2). Blackbanded darter and turquoise darter fed predominantly on larval Ephemeroptera, Trichoptera, and Diptera whereas northern hogsucker preyed almost exclusively on chironomid larvae. The diets of omnivores (bluehead chub and yellowfin shiner) included a mixture of aquatic and terrestrial invertebrates, detritus, and aquatic and terrestrial plant matter. Omnivores exhibited strong seasonal differences in diet, consuming more terrestrial plant matter (leaves, flowers, and seeds) in spring compared with detritus, aquatic and unidentified plant matter, and invertebrates in autumn (Fig. 1).

Nonmetric multidimensional scaling analysis identified three major gradients explaining the majority of variance (87%) among gut contents (Fig. 2). The axis-1 (20% variance) gradient contrasted chironomid versus terrestrial invertebrate consumption, primarily by northern hogsucker and yellowfin shiner respectively. Axis-2 (43% variance) contrasted macroinvertebrate versus plant consumption and clearly separated predators from omnivores (Fig. 2a). Rosyface chubs were generally intermediate between omnivores and predators, but tended to plot more closely with omnivores. Axis-3 (24% variance) described a gradient of increasing plant consumption and separated autumn versus spring gut contents among omnivores (Fig. 2c). MRPP tests indicated that predators and omnivores had significantly different diets and that omnivore diets were significantly different between

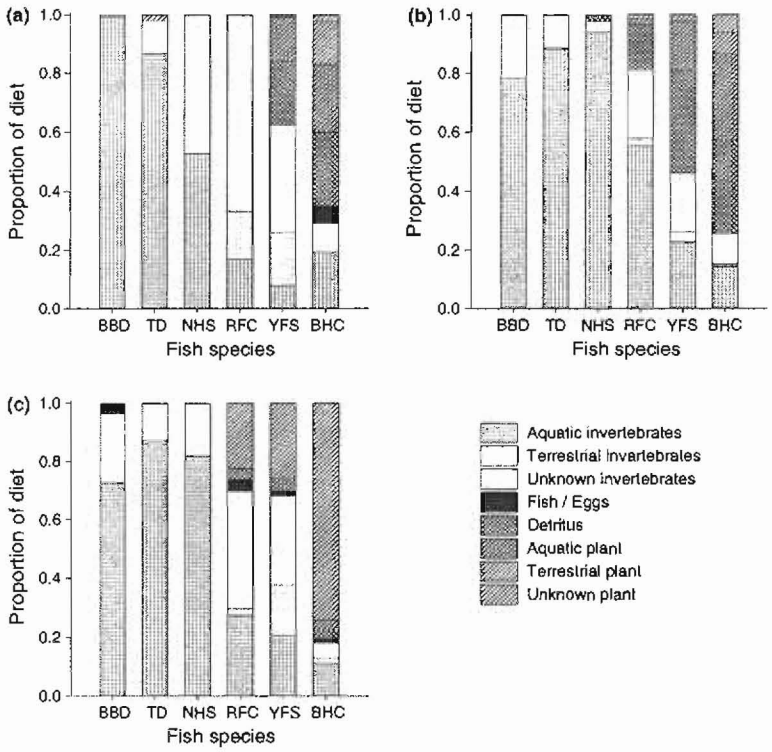

Fig. 1. Average relative proportion of gut contents for blackbanded darter (BBD), turquoise darter (TD), northern hogsucker (NHS), rosyface chub (RFC), bluehead chub (BHC) and yellowfin shiner (YFS) during autumn 2003 (a), autumn 2004 (b) and spring 2004 (c). Invertebrate taxa were grouped as single food categories to more clearly illustrate differences among species and between seasons.

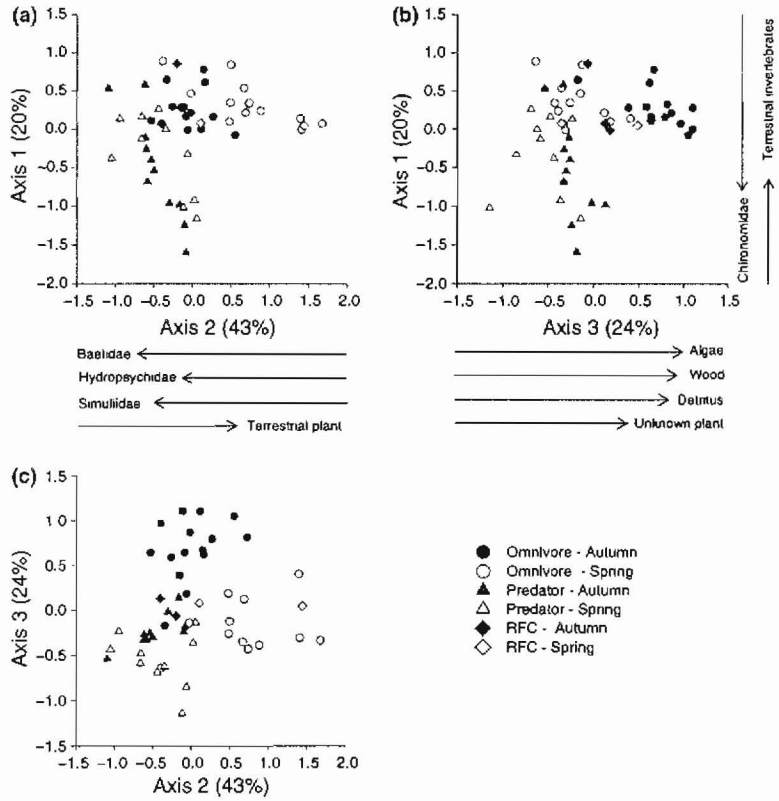

Fig. 2. Nonmetric multidimensional scaling plots of dietary data. Numbers in parentheses indicate the amount of variance explained by each axis. Predators include blackbanded darter (BBD), turquoise darter (TD), and northern hogsucker (NHS), and omnivores include bluehead chub (BHC) and yellowfin shiner (YFS). Rosyface chub (RFC) is plotted separately. Each point represents a single species-by-site-by-season observation calculated from the mean proportion of gut items. Food items shown are correlated with axes scores at $r > 0.5$.

Table 1. Multiple-response permutation procedure (MRPP) tests of trophic group and seasonal differences in diet.

Between-group comparison	T	A	P-value
Omnivores versus RFC	−0.302	0.004	0.309
Predators versus RFC	−3.775	0.049	0.005
Omnivores versus predators	−13.691	0.126	0.000
Omnivores, spring versus autumn	−10.927	0.160	0.000
Predators, spring versus autumn	−0.365	0.007	0.273

The T statistic is analogous to the Student's t-test and describes separation between groups. More negative values for T indicate stronger separation (McCune & Grace 2002). The A statistic measures chance corrected within-group agreement. Possible values of A range from 0 (no separation between groups) to 1 (complete separations between groups), with small values (~0.1) associated with significantly different ecological groups. Autumn 2003 and 2004 samples were pooled for seasonal comparisons.

spring and autumn (Table 1). Rosyface chub diet was weakly distinguished from predators, but was not significantly different from that of omnivores.

Trophic position estimates

TP_{GCA} varied significantly among species (d.f. = 5, MS = 1.80, $F = 31.15$, $P \leq 0.001$; Fig. 3a). *Post hoc* Tukey's test revealed that predators comprised one homogeneous subset, although bluehead chub and yellowfin shiner, both omnivores, differed significantly from one another. Rosyface chub was not different from either predators or yellowfin shiner. Seasonal differences in TP_{GCA} within each species were not significant (d.f. = 2, MS = 0.06, $F = 1.08$, $P = 0.35$), nor was the interaction of species and season (d.f. = 10, MS = 0.04, $F = 0.63$, $P = 0.78$).

TP_{SIA} also varied significantly among species (d.f. = 5, MS = 1.57, $F = 9.61$, $P \leq 0.001$; Fig. 3b). Differences within feeding guilds were not significant, and TP_{SIA} of predators was significantly higher than that of omnivores. Again, rosyface chub was intermediate and did not differ from either predators or yellowfin shiner. Seasonal TP_{SIA} variation within each species was significant (d.f. = 3, MS = 1.90, $F = 11.62$, $P \leq 0.001$). However, these differences did not follow a spring versus autumn pattern. TP_{SIA} in autumn 2003 was significantly lower than for spring 2003, spring 2004, and autumn 2004 for all species. The species × season interaction was not significant (d.f. = 10, MS = 0.05, $F = 0.31$, $P = 0.99$).

Comparison of GCA and SIA

TP_{GCA} and TP_{SIA} differed significantly for bluehead chub (d.f. = 12, $t = -3.21$, $P \leq 0.01$), but not for blackbanded darter (d.f. = 5, $t = 0.34$, $P = 0.74$), turquoise darter (d.f. = 7, $t = -1.81$, $P = 0.06$), northern hogsucker (d.f. = 6, $t = 1.27$, $P = 0.25$), rosyface chub (d.f. = 3, $t = 0.70$, $P = 0.53$), or yellowfin shiner (d.f. = 12, $t = 0.28$, $P = 0.78$). Range and variation in

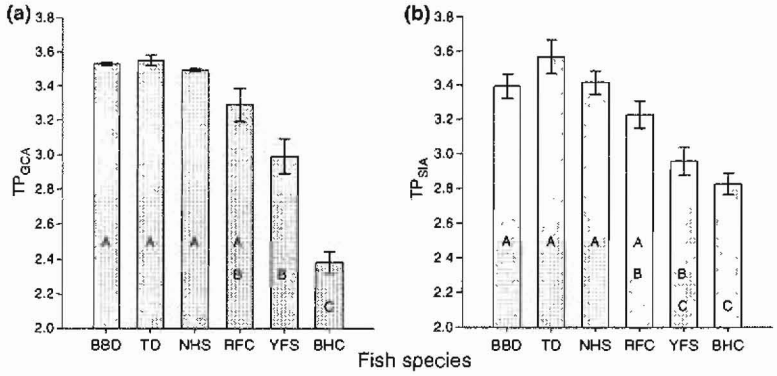

Fig. 3. Among-species difference for gut content (TP_{GCA}, 3a) and stable isotope derived (TP_{SIA}, 3b) trophic position for fishes in the Twelvemile Creek system. Data for all sites and seasons were pooled to illustrate among-species variation. Homogeneous subsets are grouped by capital letters (i.e., A, B, C). Error bars show ±1 SE. Abbreviations for species are provided in Fig. 2.

TP estimates varied between methods for each feeding guild. Omnivore TP was similar between methods (TP_{GCA} range = 2.1–3.5, CV = 16.1% and TP_{SIA} range = 2.1–3.4, CV = 14.8%), but predator TP_{GCA} was invariant (range = 3.5–3.7, CV = 1.8%) compared with TP_{SIA} (range = 2.5–4.1, CV = 12.8%). Likewise, variation in rosyface chub TP was much lower when calculated as TP_{GCA} (TP_{GCA} range = 3.0–3.5, CV = 5.9% and TP_{SIA} range = 2.7–3.4, CV = 13.5%).

Discussion

Dietary analysis supported literature descriptions of fish diets, and identified blackbanded darter, turquoise darter, and northern hogsucker as predators and yellowfin shiner and bluehead chub as omnivores. Ordination analysis identified strong differences between predator and omnivore diets, but rosyface chub did not fit neatly within either group. They consumed 80% invertebrate prey, a level consistent with a predator or invertivore trophic guild (Franssen & Gido 2006). However, their diet was more similar to omnivores than predators, which all consumed >98% invertebrate prey. Differences in feeding habits were observed among species within trophic groups. Predatory fishes were trophically similar, but northern hogsucker occupied a niche slightly different from that of blackbanded darter and turquoise darter. Diets of blackbanded darter and turquoise darter were dominated by larval benthic invertebrates such as hydropsychid caddisflies and blackflies, whereas northern hogsucker fed almost exclusively on chironomid larvae. Omnivore diets also varied slightly between species. Bluehead chub consumed more plant matter and fewer invertebrates (both aquatic and terrestrial) than yellowfin shiner.

Omnivore diets shifted from consumption of terrestrial plant matter in spring to more detritus and aquatic plant matter in autumn. Cloutman & Harrell (1987) observed similar seasonal diet shifts in the diet of whitefin shiner (*Cyprinella nivea*). This omnivorous minnow consumed 44% terrestrial plant matter in spring samples versus 3% in autumn samples in a South Carolina stream. Seasonal variation in the diet of yellowfin shiner tracks seasonal availability of food sources (Reisen 1972), and this is a likely explanation for the seasonal shifts we observed in this study. This was the first known dietary study of rosyface chub and the results revealed that it was trophically intermediate to predators and omnivores. Rosyface chub primarily consumed aquatic invertebrates and lesser amounts of aquatic and terrestrial plant matter. Rosyface chub underwent significant seasonal changes in diet similar to that of omnivores, and its diet was more similar to omnivores than predators. While rosyface chub was predaceous in the strictest sense, its TP was indistinguishable from either predators or omnivores.

TP_{SIA} and TP_{GCA} both tracked among-group differences in resource utilisation identified through direct gut analysis. Our findings contradict those of Franssen & Gido (2006) who found that TP_{SIA} did not distinguish among algivore/detritivore, omnivore, and invertivore trophic groups from four streams in Kansas, Oklahoma and New Mexico (USA). Their trophic classifications were literature-based and the results were partially related to incongruity between these classifications and gut contents in fishes they analysed. Likewise, Franssen & Gido (2006) found a higher degree of omnivory among invertivore predators than we observed. The diets of fishes in our study corresponded to literature-based trophic classification and predators showed little omnivory; hence, both TP_{SIA} and TP_{GCA} were able to clearly distinguish between omnivore and predator trophic groups.

Trophic position estimates within species were similar between methods with the exception of bluehead chub (TP_{GCA} = 2.4 vs. TP_{SIA} = 2.8). These differences could be attributed to differential assimilation of gut items, with bluehead chub deriving more energy from invertebrate prey than expected from its diet. Likewise, these differences could be explained by higher $\delta^{15}N$ fractionation rates for bluehead chub. Post (2002) and McCutchan et al. (2003) presented a mean

fractionation of 3.4 for various consumers, but variation in fractionation rates among species is large. Controlled feeding experiments are the only way to accurately measure trophic fractionation rates, and these types of studies are lacking for most fishes. TP_{GCA} yielded nearly identical estimates for all predators (TP = ~3.5). Low variance in TP_{GCA} estimates for predators was a function of assigned food source TP, as most invertebrate TP values used in the calculations were 2.5 (Vander Zanden et al. 1997).

Neither TP_{GCA} nor TP_{SIA} tracked seasonal changes observed in omnivore diets. This is not surprising given that seasonal shifts reflected differential utilisation of resources in similar TPs (i.e., greater terrestrial plant consumption in spring vs. aquatic plant and detritus consumption in autumn). Plant matter and detritus were assigned identical TPs (i.e., 1), so no seasonal differences in TP_{GCA} were detected. As these resources had similarly low $\delta^{15}N$ values, TP_{SIA} of omnivores also showed no consistent differences between spring and autumn. We would expect seasonal changes in TP only if omnivores had increased their consumption of aquatic macroinvertebrates, which occupy a higher trophic level than plant and detritus material. These findings suggest that seasonal variation in diet within-species is less important than among-species variation in diet in determining TP of stream fishes.

The use of $\delta^{15}N$ to estimate TP is uncommon in lotic studies compared to those in lentic and marine systems (Jardine et al. 2006). Selection of baseline indicators in streams is challenging because wide-ranging, long-lived, ubiquitous primary consumers are rare and omnivory among so-called primary consumers is commonplace (Jardine et al. 2006; Anderson & Cabana 2007). Our predator TP_{SIA} values (range 3.4–3.6) are consistent with those reported for invertivorous stream fishes from Oklahoma, Kansas and New Mexico (mean 3.4, Franssen & Gido 2006) and for insectivorous catostomids, cyprinids and percids in New Brunswick (mean 3.6, Anderson & Cabana 2007). These results were similar even though different baseline indicators were used [i.e., scrapers (Anderson & Cabana 2007); chironomids (Franssen & Gido 2006); primary consumers, this study]. Thus, while the selection of baseline indicator is critical, TP_{SIA} may provide a common currency for large-scale, cross-system comparisons of trophic structure and energy flow in disparate lotic ecosystems.

The results of this study highlight the power of using both GCA and SIA to identify trophic relationships among consumers. GCA confirmed literature based trophic assignments of fishes and identified subtle difference in diets for species within trophic guilds. Both methods were equally robust at discriminating trophic groups of stream fishes, but TP_{SIA} is less laborious and expensive to calculate. TP_{SIA} is increasingly used to characterise trophic relationships and to track flux of energy and matter in aquatic food webs. For example, TP has been used to assess the role of anthropogenic disturbance and trophic structure in lakes assessed at the regional scale (Cabana & Rasmussen 1994, 1996) and to quantify biomagnification of persistent organic contaminants in lentic and marine systems (reviewed in Jardine et al. 2006). Comparable studies in streams are currently lacking, but our results suggest that TP_{SIA} can be used to address similar issues in lotic ecosystems.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1. Number of guts (n), mean fish length ±1 standard deviation and size range for samples collected in spring 2004 (S04), autumn 2003 (A03), and autumn 2004 (A04) for blackbanded darter (BBD), turquoise darter (TD), northern hogsucker (NHS), rosyface chub (RFC), bluehead chub (BHC), and yellowfin shiner (YFS). Data were pooled among sites.

Appendix S2. Mean per cent gut contents from samples collected in spring and autumn for blackbanded darter (BBD), turquoise darter (TD), northern hogsucker (NHS), rosyface chub (RFC), bluehead chub (BHC), and yellowfin shiner (YFS). Data were pooled among sites.

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