



Seasonal consumption of terrestrial prey by a threatened stream fish is influenced by riparian vegetation

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ABSTRACT: The consumption of terrestrial prey by fishes highlights the functional value of terrestrial habitats, but such consumption is not well documented for many small-bodied species. We determined the diet and consumption of terrestrial prey by a threatened fish, silver shiner *Notropis photogenis*, using stomach content and stable isotope analyses to better understand the functional role of riparian habitat for the species. Results indicate silver shiner is a generalist drift feeder that consumes a wide range of aquatic and terrestrial prey. Both stomach content and stable isotope analyses indicated that terrestrial prey was commonly exploited and that terrestrial prey consumption was both seasonally and spatially variable. Based on stomach contents, the contribution of terrestrial prey was (average \pm SD) $41.53 \pm 32.35\%$ in fall and $20.45 \pm 20.45\%$ in summer; based on stable isotopes it was $35.24 \pm 4.41\%$ in fall and $39.88 \pm 12.34\%$ in summer. During fall, when bankside terrestrial invertebrates were more abundant, silver shiner stomachs contained significantly more terrestrial prey in reaches where riparian vegetation cover was highest, indicating that intact riparian cover may facilitate access to high-quality prey. The consumption of terrestrial prey may be particularly important in fall, as it may promote increased growth and survival leading to more successful overwintering. Our findings suggest that terrestrial subsidies are ecologically valuable for silver shiner and that the protection of reaches with intact riparian habitats would likely improve conservation and recovery efforts by helping ensure access to key prey resources.

KEY WORDS: Cross-ecosystem resources · Diet · Freshwater fishes · Stable isotopes · Terrestrial–aquatic linkages · Threatened fishes

1. INTRODUCTION

Aquatic systems have strong functional dependencies on terrestrial inputs for both primary and secondary production (Nakano & Murakami 2001, Taylor et al. 2013, Tanentzap et al. 2017). In temperate systems, riparian habitat and its associated terrestrial prey are important for the diet of many stream fishes (Reisen 1972, Sullivan et al. 2012), including imperilled species such as redbside dace *Clinostomus elongatus* (Daniels & Wisniewski 1994). Terrestrial prey can enhance fish production (Edwards & Huryn

1996) and facilitate resource partitioning among co-occurring species (Dineen et al. 2007, Sánchez-Hernández & Cobo 2016). Thus, terrestrial–aquatic linkages are crucial for a wide range of freshwater fishes. To maximize effective conservation, it is imperative to understand the functional role of the riparian zone on the feeding ecology of imperilled fishes, which can better inform the identification of critical habitat.

The exploitation of terrestrial prey by stream fishes highlights the functional value of adjacent terrestrial habitat (i.e. Nakano & Murakami 2001, Correa &

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Winemiller 2018); however, the link between riparian habitat, the availability of terrestrial resources, and consumption is not well understood for many species (Sullivan et al. 2012). Terrestrial prey resources, including terrestrial insects and emerged adult winged insects with aquatic larval stages (hereafter collectively referred to as 'terrestrial prey') are essential cross-ecosystem resources that become entrained in the surface flow from surrounding riparian habitats (Grunblatt et al. 2019). Utilization of terrestrial prey accessed from surface flow is common and well documented for some salmonid species (Nakano & Murakami 2001, Romaniszyn et al. 2007, Eberle & Stanford 2010, Sánchez-Hernández & Cobo 2016) but remains poorly studied for many small-bodied fishes, particularly imperilled species. Consumption of terrestrial prey may have important positive effects on the growth and persistence of fishes given that it is typically of higher energy density relative to aquatic prey such as the aquatic larval forms of emergent insects (Francis & Schindler 2009). Therefore, it is important to identify factors that affect the availability and consumption of terrestrial prey by fishes other than salmonids, particularly small-bodied drift-feeding fishes.

Threats such as urbanization can negatively impact terrestrial prey subsidies to aquatic systems by altering riparian habitat (Francis & Schindler 2009), which can reduce the supply of, and access to, terrestrial prey. The quality and type of riparian canopy along a streambank can have profound influences on the supply and consumption of terrestrial prey by stream fishes (Edwards & Huryn 1996, Ryan & Kelly-Quinn 2015). Sparsely vegetated riparian zones are associated with reduced supply of terrestrial prey to the stream drift as a result of increasing the lateral dispersal of emerged adult winged insects away from the stream, reducing the probability of re-entry, and limiting the in-fall of terrestrial invertebrates (Briers & Gee 2004, Grunblatt et al. 2019). Evaluating how differences in riparian vegetation cover impact prey supply, and in turn the feeding habits of stream fishes, is thus essential for understanding the effect of riparian changes on the feeding ecology of fishes. However, for many small-bodied freshwater fishes basic information is lacking on diet and feeding habits, which restricts the ability of conservation managers to assess the biological responses of such fishes to reductions or improvements in riparian habitat quality.

Silver shiner *Notropis photogenis* is a small-bodied freshwater minnow (approximate maximum length: 144 mm; Bouvier et al. 2013) listed as threatened under Canada's Species at Risk Act. Within Canada,

silver shiner exists at the northern edge of its North American range and faces increasing urbanization pressure (Stanfield & Kilgour 2006, Ontario Ministry of Finance 2019, Burbank et al. 2020). The diet of silver shiner in Canada is poorly understood, based on a few field observations (Baldwin 1983) and gut content analysis of a limited number of individuals (Gruchy et al. 1973, n = 9; McKee & Parker 1982, n = 35). Limited examination of the feeding habits of silver shiner (n = 5) captured among a complex sympatric minnow community in the New River, North Carolina, indicated that individuals exploited terrestrial prey (~45% of diet; Burress et al. 2016). Based on these limited feeding observations, it is unclear to what extent such consumption patterns hold temporally or spatially for silver shiner, particularly at the northern edge of its range in Canada where differences in fish community composition may lead to different competitive dynamics relative to southern populations, and thus potential differences in the reliance on terrestrial prey. Therefore, improved understanding of terrestrial prey consumption by silver shiner will help identify important terrestrial-aquatic linkages likely to benefit the identification of critical riparian habitat and broader recovery actions for this threatened species in Canada.

Here, we determined the diet and consumption of terrestrial prey by silver shiner using stomach content and stable isotope analyses to better inform the functional role of the riparian zone for the species. Given the suspected importance of terrestrial prey, we provide a general description of the diet of silver shiner across multiple seasons, and test the hypotheses that (1) silver shiner has a broad feeding niche typical of generalist drift-feeding fishes, (2) within the feeding niche, silver shiner demonstrate reliance on terrestrial prey, (3) terrestrial consumption varies seasonally, increasing in the fall, (4) relative bank-side terrestrial invertebrate abundance is positively correlated with upstream riparian cover, (5) terrestrial consumption varies positively with upstream riparian cover, and (6) terrestrial consumption is higher in adults (ages 1 and greater) than in juveniles (age 0).

2. MATERIALS AND METHODS

2.1. Field sampling

Silver shiner was captured (n = 1941) in 3 river reaches (Fig. 1) within Sixteen Mile Creek, Oakville, Ontario (43° 27' 40.6" N, 79° 45' 26.7" W) during summer (17–26 July) and fall (18–22 September) 2017.

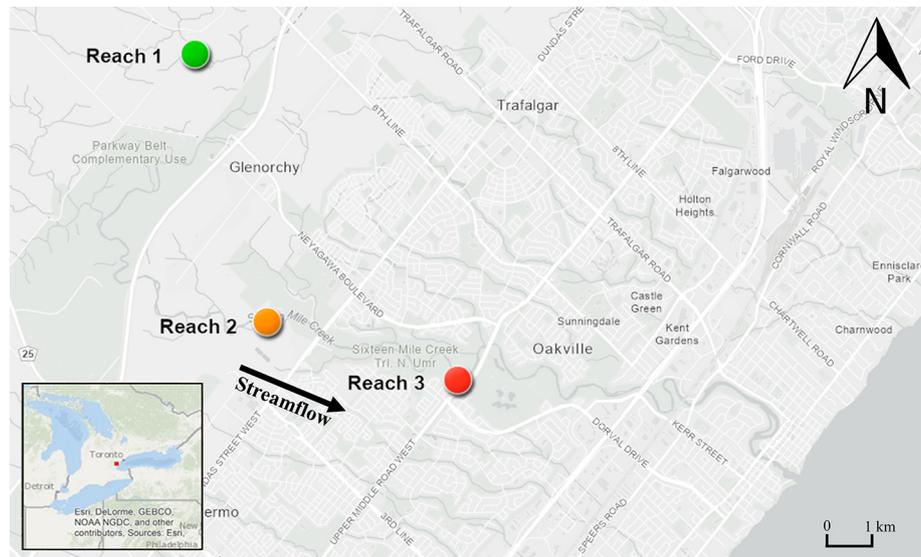


Fig. 1. Study area showing reach 1 (green), reach 2 (orange), and reach 3 (red) where silver shiner were captured in Sixteen Mile Creek, Oakville, Ontario, Canada

Reaches were spread across approximately 12.5 km (with 6–7 km between one another) and were numbered sequentially from upstream (reach 1) to downstream (reach 3). The separation between each reach was presumed to prevent the movement of individual fish among reaches given the limited linear home ranges (42.9–79 m) estimated for a similar species, yellowfin shiner *N. lutipinnis* (Goforth & Foltz 1998), and small-bodied fishes in general (Minns 1995, Woolnough et al. 2009). Fish were captured with 3 repeat hauls of a 9.14 m bag seine net (3 mm mesh). A subset of captured individuals ($n = 180$; $n = 30$ from each reach in summer and fall) were euthanized, placed on ice at capture, and stored in the freezer (-20°C) upon returning to the laboratory. All fishes were collected and retained under an animal use permit (AUP 1846) approved by the Canadian Council on Animal Care. Following fish collections, measures of stream width (m), depth (m), water velocity (m s^{-1}), pH, dissolved oxygen (mg l^{-1}), and water temperature ($^{\circ}\text{C}$) were taken at each sampling location (Table 1). Furthermore, samples of potential

prey, algae, and terrestrial vegetation were collected at each sample location for stable isotope analysis. Samples of potential prey items within the stream were collected with a 3 min kick and sweep sampling method at each sampling site using a D-net, following the Canadian Aquatic Biomonitoring Network (CABIN) protocol (Environment Canada 2012). Potential terrestrial prey items were collected along the streambank adjacent to each sample location by swinging a sweep net along 5 parallel transects approximately 10 m in length (Kogan & Henry 1980, Anderson et al. 2013). As the sample sites were easily accessible from nearby urban areas, drift nets were not used to collect instream drift samples due to the potential for tampering or removal during extended net sets. Additionally, algae were scraped from rocks and the 3 most common terrestrial vegetation species present at each sample location were collected for stable isotope analysis.

The average percent riparian vegetation cover from each sample location to 1 km upstream from the capture location was estimated using satellite imagery

Table 1. Measures of mean stream width, depth, water velocity, pH, dissolved oxygen (DO) and water temperature ($^{\circ}\text{C}$) taken at each sample location following silver shiner collections

Habitat variable	Reach 1		Reach 2		Reach 3	
	Fall	Summer	Fall	Summer	Fall	Summer
Mean stream width (m)	12.00	16.17	8.00	12.00	13.00	16.50
Mean depth (m)	0.35	0.31	0.40	0.48	0.33	0.34
Mean water velocity (m s^{-1})	0.11	0.18	0.28	0.29	0.23	0.28
Mean pH	8.45	8.40	8.32	8.30	8.53	8.56
Mean DO (mg l^{-1})	8.93	10.26	8.11	8.78	9.81	11.37
Mean water temperature ($^{\circ}\text{C}$)	20.43	23.20	19.28	21.26	18.89	20.94

(Dala-Corte et al. 2017) obtained from Google Earth (version 7.3; accessed 22 July 2020). Terrestrial vegetation cover in squares of $\sim 100 \times 100$ m on each side of the stream was examined and percent cover (ranging from 0–100%) was estimated as a proportion of the sample square starting at the sampling location and working upstream. The average of all 20 squares (10 per stream bank) was taken to estimate the mean percent terrestrial cover and associated standard deviation at each sampling location.

Once in the lab, fish were thawed, total length (mm) and mass (g) were measured, and the entire gastrointestinal tract was removed and placed in 95% ethanol for gut content analysis. A sample of dorsal muscle tissue was also retained for carbon stable isotope analysis ($\delta^{13}\text{C}$).

2.2. Stomach content analysis

Numeric gut content analyses (counts) of a subset of individuals ($n = 165$; $n = 90$ from summer 2017 and $n = 75$ from fall 2017) were completed using standard methods as described in Hyslop (1980). Prey items were examined under a dissecting microscope, identified to the lowest practical taxonomic level (usually genus), and classified as aquatic or terrestrial at the time of consumption. Because our intent was to evaluate the proportion of diet that came from riparian habitats, prey items with aquatic larval stages but consumed as emerged winged adults in the terrestrial phase were classified as terrestrial following Milardi et al. (2016). Prey items were then sorted into terrestrial and aquatic prey groups for statistical analyses. The terrestrial groups included barkflies (Order Pscocodea), jumping plant lice (Family Psyllidae), miscellaneous terrestrial insects (Class Insecta), terrestrial beetles (Order Coleoptera), terrestrial Diptera (Order Diptera), wasps and ants (Order Hymenoptera), adult emerged caddisflies (Order Trichoptera), and adult emerged Chironomidae (Family Chironomidae). The aquatic groups included aquatic beetles (Order Coleoptera), larval caddisflies (Order Trichoptera), larval mayflies (Order Ephemeroptera), other larval midges (including Families Empididae, Simuliidae, Tipulidae, and Chironomidae and Subfamilies Chironominae, Orthocladiinae, and Tanypodinae), and Chironomidae pupae (Family Chironomidae). Rarely consumed prey items with less than 7 items found across all stomachs ($<0.26\%$ of total consumed prey) were excluded from analyses as they were not considered relevant prey items.

The relative proportions of each prey group consumed by all individuals at each reach in fall and summer were calculated. Additionally, the relative percent availability of terrestrial invertebrate groups along the streambank was estimated using the swing sweep samples. Similarly, the relative percent availability of benthic invertebrate groups along the streambed was estimated using the 3 min kick and sweep samples. To examine the relative amount of bankside terrestrial invertebrates collected at each reach in fall and summer, the relative abundance of terrestrial streambank invertebrates was estimated using the swing sweep samples. Further, the correlation between the relative abundance of bankside terrestrial invertebrates and the average percent riparian vegetation cover was evaluated by calculating Pearson's correlation coefficient (Zar 2010).

The niche breadth of silver shiner at each reach in fall and summer was computed using Levins' Index (Levins 1968, Krebs 2014). Additionally, generalist vs. specialist feeding strategies were determined following Amundsen et al. (1996). Briefly, the frequency of occurrence (FO) of each prey group was calculated as:

$$\text{FO}_i = \frac{N_i}{N_T} \quad (1)$$

where N_i is the number of silver shiner stomachs sampled that contained prey i and N_T is the total number of silver shiner stomachs sampled. FO was then plotted against the prey-specific-abundance (P_i), computed as:

$$P_i = \left(\frac{\sum S_i}{\sum S_T} \right) \times 100 \quad (2)$$

where S_i is the total number of prey group i found in all examined stomachs and S_T is the total number of prey items found in all individuals with prey i in their stomach. Plots of FO_i versus P_i identified the feeding strategies of silver shiner at each reach and season, with prey groups plotting towards the top indicating specialization and prey groups found near the bottom signifying generalist feeding behavior (Amundsen et al. 1996, Burbank et al. 2019).

Additionally, to evaluate the importance of terrestrial prey, stomach content results were used to calculate the percent contribution of terrestrial prey to the diet of each individual silver shiner ($\text{TC}\%_{\text{SC}}$). $\text{TC}\%_{\text{SC}}$ was compared among (1) seasons at each reach and (2) reaches within each season to determine if $\text{TC}\%_{\text{SC}}$ varied seasonally and spatially. The comparison among seasons was conducted with a 2-sample 1-tailed t -test to determine if average $\text{TC}\%_{\text{SC}}$

in silver shiner diets was significantly higher in fall compared to summer. Reach comparisons were conducted using 1-way ANOVA, with the assumptions of normality and homoscedasticity evaluated using the Shapiro-Wilk's *W*-test and graphs of residual versus fitted values respectively (Zar 2010). Lastly, we used a 2-sample 1-tailed *t*-test to examine if adult (ages 1 and greater) average TC%_{SC} was significantly higher than the average TC%_{SC} estimated for juveniles (age 0). The age of individual fish was determined using an age-length key previously developed for the species (Burbank et al. 2021). If assumptions of the parametric tests were not met, the non-parametric Mann-Whitney *U*-test and Kruskal-Wallis test were used in place of the *t*-test and 1-way ANOVA, respectively.

2.3. Stable isotope analysis

Silver shiner dorsal muscle tissue samples, algae, and terrestrial vegetation samples were dried at 50°C for 48 h in a laboratory drying oven (Yamato DX 600; Yamato Scientific Company), weighed, and analyzed for $\delta^{13}\text{C}$ at the University of Waterloo Environmental Isotope Laboratory using a Delta Plus continuous-flow isotope ratio mass spectrometer (Thermo Finnigan) coupled to an ECS 4010 Elemental Analyzer (Costech Analytical Technologies) with an analytical precision of $\pm 0.2\text{‰}$. Stable isotope results are expressed in delta notation (δ) as parts per thousand differences (‰) with respect to the international reference standards Vienna Peedee Belemnite (Craig 1957). Analytical precision was established with the use of internal laboratory standards cross-calibrated against International Atomic Energy Agency standard (CH6) at the beginning, middle, and end of all sample runs.

Stable isotope analysis provides a powerful means of estimating the relative contributions of terrestrial and aquatic carbon sources to individual organism diets because such sources often have distinctive isotopic compositions (Kendall et al. 2001). Stable isotope analysis evaluates diet over a longer temporal scale (i.e. months; Boecklen et al. 2011, Colborne et al. 2017) compared to stomach content analysis, which offers a much shorter temporal snapshot of an individual's diet (Hyslop 1980). We implemented both approaches here to evaluate terrestrial prey consumption over multiple temporal scales. We used $\delta^{13}\text{C}$ values to evaluate the relative contribution of terrestrial carbon sources to the diet of silver shiner individuals using a 2-source single isotope ($\delta^{13}\text{C}$)

mixing model (Phillips & Gregg 2001), following Grey & Jones (2001), Bunn et al. (2003), Finlay & Vredenburg (2007), Abrantes & Sheaves (2010), and Akamatsu & Toda (2011). Aquatic end member $\delta^{13}\text{C}$ values required for the model consisted of algae scraped from rocks collected from each reach, and the terrestrial end member consisted of common C3 riparian vegetation collected adjacent to each sampling location. The average terrestrial contribution to the diet of silver shiner estimated from stable isotopes (TC%_{SI}) was compared among (1) seasons at each reach and (2) reaches within each season in a manner identical to the TC%_{SC} estimates. Lastly, we used a 2-sample 1-tailed *t*-test to examine if adult (ages 1 and greater) average TC%_{SI} was significantly higher than juvenile (age 0) average TC%_{SI}. All analyses were conducted in R version 3.6.1 (R Development Core Team 2019).

3. RESULTS

A total of 2751 organisms from aquatic and terrestrial environments representing 74 taxa were collected and identified from 165 stomachs. Only 6 individuals were found to have empty stomachs. On average, individual stomachs contained 5.7 different taxa and 16.7 identifiable organisms. The largest number of organisms found in one silver shiner was 56.

In summer 2017, silver shiner consumed a high average relative abundance of other midges (41.02%), mayflies (27.93%), and emerged adult Chironomidae (11.91%). In fall 2017, silver shiner also consumed a high average relative abundance of other midges (24.66%), mayflies (23.19%), and emerged adult Chironomidae (18.88%). The relative abundance of consumed prey varied among reaches and seasons and was generally reflective of the relative availability of terrestrial and aquatic invertebrates (Fig. 2). Silver shiner consumed the highest relative abundance of emerged adult Chironomidae in fall 2017 at reach 1 (29.66%) and reach 3 (37.86%; Fig. 2, Table 2), where the relative availability of emerged adult Chironomidae along the streambank was highest. The niche breadth (Levins' Index) in fall was 5.59 at reach 1, 4.24 at reach 2, and 4.70 at reach 3. During summer the niche breadth of silver shiner was 5.39 at reach 1, 2.58 at reach 2, and 3.33 at reach 3. Typically, silver shiner exhibited generalist feeding tendencies, where the majority (>50%) of individuals consumed a variety of prey items and did not specialize on any one prey group (Fig. 3). Slight specialization was observed during summer at reaches 2 and 3

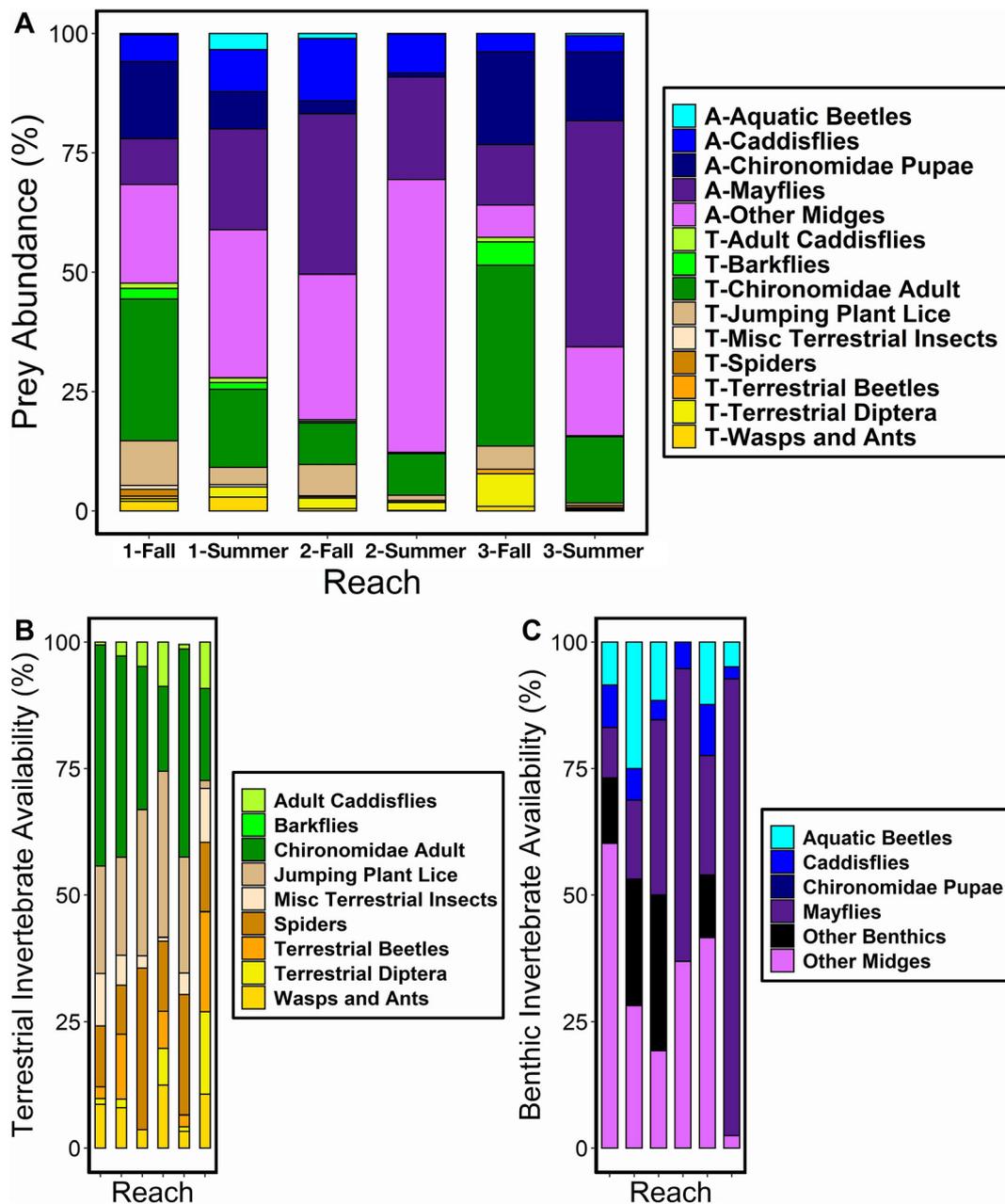


Fig. 2. (A) Abundance (%) of prey groups identified in the stomach contents of silver shiner captured at reaches 1, 2, and 3 in fall and summer 2017, (B) relative availability of bankside terrestrial invertebrates (%) in the riparian area adjacent to reaches 1, 2, and 3 in fall and summer 2017 estimated using swing-sweep samples, and (C) relative availability of benthic invertebrates (%) in the benthic regions of reaches 1, 2, and 3 in fall and summer 2017 estimated using the kick and sweep samples. The order of the x-axis labels in (A) also applies to (B) and (C). The 'Other Benthics' group consists of larval Anisoptera, Zygoptera, Plecoptera, Megaloptera, and Tabanidae

on the other midges and mayflies prey group, respectively (Fig. 3).

Overall, silver shiner $TC\%_{SC}$ was $41.53 \pm 32.35\%$ (average \pm SD) in fall and $20.45 \pm 20.45\%$ during the summer, but ranged from 0–100% (Fig. 4). Average riparian vegetation cover was significantly different among reaches (Kruskal-Wallis test, $\chi^2 = 13.40$, $p <$

0.05) and was highest at reaches 1 ($79 \pm 13.44\%$) and 3 ($77 \pm 13.29\%$) and lowest at reach 2 ($61 \pm 16.57\%$). Average riparian vegetation cover was positively correlated with the relative abundance of bankside terrestrial invertebrates (Pearson's $r = 0.705$; Fig. 5A). Silver shiner average $TC\%_{SC}$ (Table 3) was significantly higher in fall compared to summer at reaches

Table 2. Abundance (%) of each prey group identified within the stomach contents of all silver shiner individuals captured at reaches 1, 2, and 3 during fall and summer 2017. The letter preceding prey group names indicates if the group was considered aquatic (A) or terrestrial (T)

Prey group	Reach 1		Reach 2		Reach 3		Overall	
	Fall	Summer	Fall	Summer	Fall	Summer	Fall	Summer
A-Aquatic beetles	0.28	3.37	1.06	0.12	0.00	0.46	0.68	1.00
A-Caddisflies	5.65	8.89	13.10	8.17	3.88	3.48	9.59	7.16
A-Chironomidae pupae	16.10	7.69	2.65	0.82	19.42	14.39	9.00	5.93
A-Mayflies	9.60	21.15	33.63	21.47	12.62	47.33	23.19	27.93
A-Other midges	20.62	31.01	30.44	57.18	6.80	18.56	24.66	41.02
T-Adult caddisflies	1.13	0.96	0.35	0.23	0.97	0.00	0.68	0.35
T-Barkflies	2.26	1.44	0.35	0.00	4.85	0.23	1.47	0.41
T-Chironomidae adult	29.66	16.35	8.67	8.75	37.86	13.92	18.88	11.91
T-Jumping plant lice	9.32	3.61	6.55	1.05	4.85	0.46	7.34	1.53
T-Misc. terrestrial insects	0.85	0.48	0.18	0.35	0.00	0.00	0.39	0.29
T-Spiders	1.41	0.00	0.00	0.00	0.00	0.46	0.49	0.12
T-Terrestrial beetles	0.56	0.00	0.35	0.12	0.97	0.23	0.49	0.12
T-Terrestrial Diptera	0.56	2.16	2.12	1.63	6.80	0.23	2.05	1.41
T-Wasps and ants	1.98	2.88	0.53	0.12	0.97	0.23	1.08	0.82

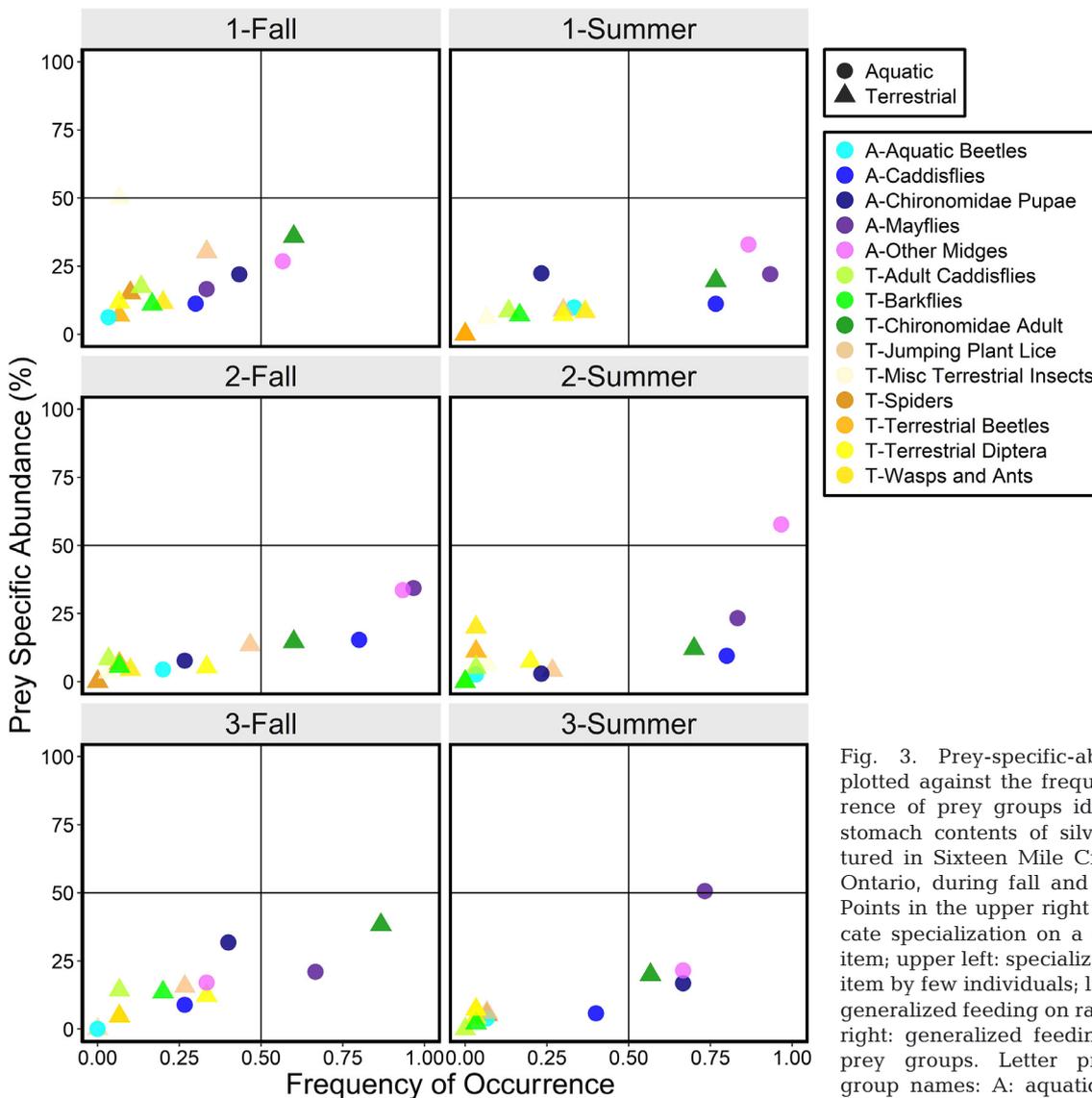


Fig. 3. Prey-specific-abundance (%) plotted against the frequency of occurrence of prey groups identified in the stomach contents of silver shiner captured in Sixteen Mile Creek, Oakville, Ontario, during fall and summer 2017. Points in the upper right quadrant indicate specialization on a dominant prey item; upper left: specialization on a prey item by few individuals; lower left: more generalized feeding on rarer prey; lower right: generalized feeding on common prey groups. Letter preceding prey group names: A: aquatic; T: terrestrial

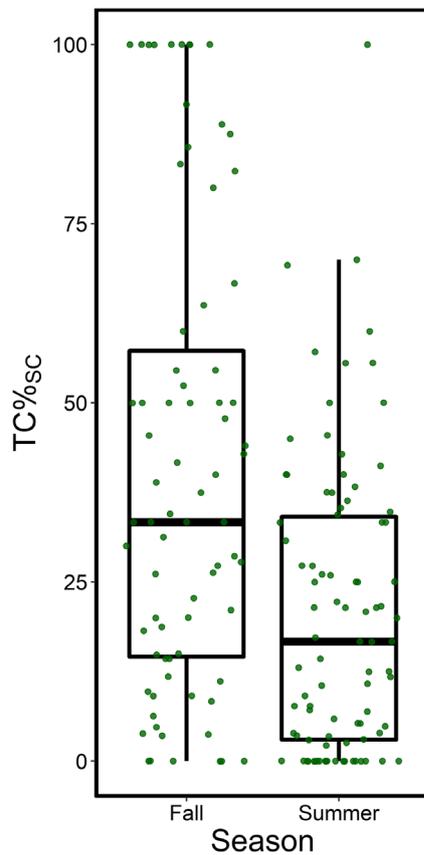


Fig. 4. Percent of silver shiner diet composed of terrestrial prey based on stomach contents ($TC\%_{SC}$) for individuals captured in Sixteen Mile Creek, Oakville, Ontario, in fall and summer 2017. Green points show individual estimates of terrestrial consumption for $n = 75$ captured in fall and $n = 90$ captured in summer. Boxplots show the median (midline), inter-quartile range (boxes), and largest values within 1.5 of the inter-quartile range (whiskers)

1 (Mann-Whitney U -test, $W = 231$, $p < 0.05$) and 3 ($W = 67.5$, $p < 0.05$) where riparian vegetation cover was highest. At reach 2, where riparian cover was lowest, the average $TC\%_{SC}$ was not significantly different between fall and summer ($W = 359.5$, $p = 0.18$; Fig. 5B). Average $TC\%_{SC}$ among reaches within each season were significantly different in both fall ($\chi^2 = 24.16$, $p < 0.05$) and summer ($\chi^2 = 14.83$, $p < 0.05$; Fig. 5B). The average adult $TC\%_{SC}$ was not significantly greater than the average juvenile $TC\%_{SC}$ in fall (t -test, $t_{11.15} = 0.586$, $p = 0.28$) and summer ($t_{56.95} = -1.32$, $p = 0.90$).

Silver shiner had an average $\delta^{13}C$ of $-26.99 \pm 0.49\text{‰}$. The $\delta^{13}C$ of aquatic algae ($-24.94 \pm 1.48\text{‰}$) and terrestrial vegetation ($-30.11 \pm 1.38\text{‰}$) were significantly different ($t_{19.91} = 8.48$, $p < 0.05$). The $TC\%_{SI}$ estimated from the 2-source single isotope ($\delta^{13}C$) mixing model ranged from 16.92 to 60.19% ($39.88 \pm$

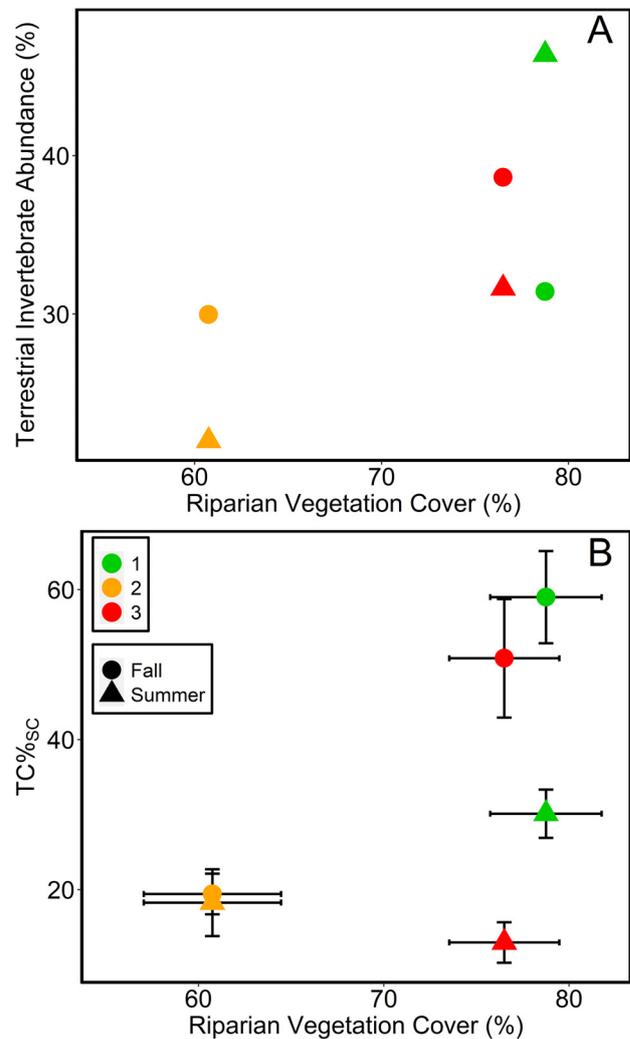


Fig. 5. Percent riparian vegetation cover and the (A) relative abundance of bankside terrestrial invertebrates (%) estimated using the swing-sweep samples in fall and summer 2017 at each reach and (B) percent of silver shiner diet composed of terrestrial prey based on stomach contents ($TC\%_{SC}$; mean \pm SE) for fish captured in fall and summer 2017 at each reach. Average $TC\%_{SC}$ was significantly higher in fall compared to summer at reaches 1 and 3 and was significantly different among reaches during fall and summer (see Section 3)

Table 3. Average (\pm SD) percent of silver shiner diet comprised of terrestrial prey based on stomach content and stable isotope analyses

Reach	Season	Stomach content	Stable isotope
1	Fall	58.99 \pm 33.65	36.58 \pm 4.99
	Summer	30.12 \pm 17.61	53.01 \pm 8.66
2	Fall	19.42 \pm 14.85	32.96 \pm 3.00
	Summer	18.27 \pm 24.39	35.11 \pm 2.99
3	Fall	50.84 \pm 30.60	37.27 \pm 3.55
	Summer	12.96 \pm 14.81	31.25 \pm 10.28

12.34%) in summer and from 25.81 to 48.73% (35.24 \pm 4.41%) in fall. The average TC%_{SI} (Table 3) at each reach differed significantly between fall and summer (all Mann-Whitney *U*-tests, $p < 0.05$). Examinations of differences in TC%_{SI} among reaches within each season indicated the average TC%_{SI} was significantly different among reaches in both fall ($\chi^2 = 15.56$, $p < 0.05$) and summer ($\chi^2 = 47.12$, $p < 0.05$). The average adult TC%_{SI} was not significantly greater than the average juvenile TC%_{SI} in fall ($t_{15.19} = 0.865$, $p = 0.20$) and summer ($t_{84.13} = -11.52$, $p = 0.99$).

4. DISCUSSION

A thorough understanding of feeding habits can help to identify important prey resources and the factors that influence prey consumption. Our results indicate that silver shiner exhibited a generalist feeding strategy, consuming a wide variety of aquatic and terrestrial prey. Terrestrial prey consumption was temporally and spatially variable, with a higher relative proportion consumed in fall than summer. Furthermore, terrestrial prey consumption was not significantly higher in adults compared to juveniles. Both stomach content and stable isotope analyses indicated terrestrial prey were commonly exploited and consumed across seasons, highlighting the importance of terrestrial-aquatic linkages for the species. Terrestrial prey consumption varied positively with upstream riparian vegetation cover, with trends stronger in fall when bankside terrestrial invertebrates were more abundant, suggesting that intact riparian habitat likely provides important terrestrial subsidies for silver shiner. Altogether, these results emphasize that silver shiner has potentially important terrestrial-aquatic linkages at its northern range boundary and that the functional role of riparian habitat should be considered when identifying and protecting critical habitat in Canada.

Generalist and opportunistic prey consumption by silver shiner was evident in the range of unique taxa consumed. The diverse diet was facilitated by exploitation of both aquatic and terrestrial prey in the surface drift (J. Burbank pers. obs.), which has been seen with other small-bodied, stream-dwelling fishes such as yellowfin shiner (Reisen 1972) and rough shiner *N. baileyi* (Mathur & Ramsey 1974). Drift-feeding fishes commonly exploit terrestrial prey, and these cross-ecosystem subsidies are important dietary sources that facilitate resource partitioning among sympatric stream-dwelling fishes. Generally, we observed a wide niche breadth for silver shiner

when individuals were accessing and consuming a wide range of terrestrial and aquatic prey. Conversely, niche breadth was narrowest during summer at reach 2, where both terrestrial consumption and riparian vegetation cover were relatively low. The exploitation of terrestrial resources by silver shiner may allow individuals to occupy a wide and unique dietary niche compared to other co-occurring fishes that are restricted to feeding lower in the water column (e.g. *Rhinichthys* spp.), thereby helping to facilitate coexistence among stream fishes.

Stomach content analysis indicated silver shiner consumed notably more terrestrial prey in fall when more terrestrial material typically enters the stream (Sagar & Glova 1992), similar to observations for juvenile coho salmon *Oncorhynchus kisutch* (Eberle & Stanford 2010). Furthermore, in fall, 9 individuals were found to have only terrestrial prey sources within their stomach, highlighting frequent and sometimes intense use of terrestrial prey. The terrestrial sweeps captured significantly more terrestrial invertebrates per sweep during fall compared to summer (*t*-test, $t_{131.67} = -1.32$, $p < 0.05$), with a total of 1872 individuals collected in fall compared to 1470 individuals in summer, suggesting there were more terrestrial prey items present along the streambanks and potentially entering the stream during fall. When bankside terrestrial invertebrates were more abundant (fall), silver shiner stomachs contained significantly more terrestrial prey at areas where riparian vegetation cover was highest (reaches 1 and 3), indicating riparian vegetation can help provide and maintain access to terrestrial prey. Conversely, during summer when less bankside terrestrial prey was present, there was a reduction in terrestrial consumption from upstream to downstream regardless of suitable riparian cover.

Exploitation of terrestrial prey may be particularly important during the fall because terrestrial prey items are energy-dense prey (Francis & Schindler 2009) that may increase growth, survival (Sullivan et al. 2012), and successful overwintering. Although limited winter feeding has been noted in stream-dwelling fishes, energy intake is often insufficient to prevent over-winter metabolic deficits (Cunjak et al. 1987, Hurst 2007), with exhaustion of energy reserves often implicated as a cause of mortality (Hurst 2007). Furthermore, small-bodied fishes may be at greater risk of over-winter mortality as a result of their higher weight-specific metabolic rates (Jobling 1993), making energy-rich fall prey consumption and pre-winter conditioning particularly important for drift-feeding fishes such as silver shiner.

Reductions in terrestrial invertebrate supply have been shown to diminish the condition and growth of some stream-dwelling fishes, depending on their reliance on terrestrial invertebrate prey (Baxter et al. 2007, Gillette 2012). Estimates of energy density found in the literature (Cummins & Wuycheck 1971, Gray 2005, Koehler et al. 2006, Francis & Schindler 2009) indicate mayflies and the terrestrial prey consumed by silver shiner contain substantially higher average energy densities (20 429 and 8137 J g⁻¹ wet weight, respectively) than the average energy densities of the remaining aquatic prey consumed (3524 J g⁻¹ wet weight), highlighting the importance of mayflies and terrestrial prey for potentially increasing energy acquisition, growth, and survival of the species. Literature values of energy densities should be viewed with caution because the energy density of invertebrates varies among systems, but the estimates nonetheless provide an indication of the relative difference in energy provided by the prey types. Given the sensitivity of mayflies to pollutants (Hubbard & Peters 1978, Krieger et al. 1996, Hamid & Rawi 2017) and the link between terrestrial prey consumption and riparian vegetation (Francis & Schindler 2009, Grunblatt et al. 2019), suitable water quality and riparian vegetation cover are likely essential to maintain the supply and consumption of energy-dense prey items by silver shiner.

Stomach content and stable isotope-based estimates indicated terrestrial prey are commonly exploited prey resources, suggesting that our overarching conclusions were robust to the chosen methods. However, observed differences between stomach content and stable isotope-based estimates were expected, as the 2 methods evaluate diet on different temporal scales; stomach content analysis can identify prey consumed hours before collection whereas stable isotope analysis integrates diet signals over several months (i.e. ~68–166 d for emerald shiner *N. atherinoides* [Colborne et al. 2017], a species morphologically similar to silver shiner). Therefore, fish captured in summer would have stable isotope values reflective of prey consumed several months prior to capture, and fall-captured individuals would reveal spring and summer feeding. Additionally, $\delta^{13}\text{C}$ values of emerged adult winged insects with aquatic larval stages incorporate isotope values from their resident time in aquatic and terrestrial environments and thus do not represent a pure terrestrial signal. Such temporal averaging would bias seasonally based computations of terrestrial reliance toward dependence on aquatic resources given the time it takes for muscle tissue to come to equilibrium with

prey resources once a dietary switch has been made (e.g. Franssen et al. 2017, Shigeta et al. 2017, Winter et al. 2019).

The functional value of intact riparian vegetation on the growth and survival of stream fishes is not well understood (Richardson et al. 2010), which limits our ability to understand how losses through land-use conversion, or gains through targeted restoration measures, influence species persistence. Nevertheless, intact riparian vegetation is imperative for numerous species including the endangered redbside dace, which has experienced range contractions associated with urbanization (Poos et al. 2012). Our results suggest that intact riparian vegetation may be important for the survival and persistence of silver shiner given the role of riparian habitats in supplying terrestrial prey to the surface flow for consumption (Collins et al. 2016, Grunblatt et al. 2019).

Grunblatt et al. (2019) determined intact shrub and forest riparian habitats led to increased consumption of terrestrial prey by retaining terrestrial and emerged adult winged insects close to the streambanks, increasing opportunities for in-fall and entrainment in surface flow. Furthermore, Kawaguchi & Nakano (2001) found the input of terrestrial prey and biomass of salmonids was higher in reaches with forest riparian cover compared to grasslands, highlighting that riparian vegetation may play an important role in determining the local distributions of fishes that exploit terrestrial prey. Silver shiner has been shown to experience reduced growth and survival in urban stream reaches (Burbank et al. 2021). Therefore, developing an understanding of how urbanization influences riparian habitat quality and associated terrestrial subsidies can further help elucidate the nature of the threats faced by species like silver shiner. Urbanization can contribute to the homogenization and reduction of riparian vegetation communities (White & Greer 2006). However, in our study riparian vegetation was abundant at some urban reaches, suggesting that targeted restoration or protection measures can provide functional riparian habitats in urban systems. When sufficient stretches of the riparian zone are conserved or restored in urbanizing areas, it appears terrestrial prey consumption and the overall diet of silver shiner can be maintained. The result points to the possible importance of local conditions and the efficacy of local conservation actions for maintaining riparian habitat. Nevertheless, future investigations should also consider other factors, including the role of other urbanization effects on aquatic food sources, as important avenues of further study for this species.

Terrestrial prey are valuable dietary items for silver shiner, as has been noted for other fishes within the genus *Notropis* (Reisen 1972, Mathur & Ramsey 1974, Matthews et al. 1978, Burress et al. 2016). In comparison to other members of the genus *Notropis*, silver shiner typically consumed higher amounts of terrestrial prey than Sabine shiner *N. sabiniae* (0–5%; Williams & Bonner 2006) and similar amounts to rosyface shiner *N. rubellus* (26.2%; Pfeiffer 1955), yellowfin shiner (28.79%; Reisen 1972), Coosa shiner *N. xanocephalus* (36.8%; Jolly & Powers 2008), and rough shiner (55.38%; Mathur & Ramsey 1974). Given the apparent importance of terrestrial prey for drift-feeding fishes such as silver shiner, the related implications for growth and survival should be further explored. Our results suggest the riparian zone is important for silver shiner as a result of its provision of valuable prey resources to silver shiner diets, and maintaining its integrity should be considered when developing conservation and recovery strategies for the species. Furthermore, our results highlight that conservation and restoration efforts for lotic systems in general should acknowledge terrestrial–aquatic linkages and the riparian zone as potentially important determinants for the feeding ecology of some small-bodied stream-dwelling fishes, including silver shiner.

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