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Terrestrial subsidies in the diets of stream fishes of the USA: comparisons among taxa and morphology

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Abstract. Terrestrial food subsidies are important energy sources to stream fishes worldwide. However, their importance is not fully understood, except perhaps for some salmonid communities. Using the published literature, we investigated patterns of fish taxonomy and jaw morphology in the consumption of terrestrial food subsidies by non-salmonid stream fishes in the USA. We hypothesised that: (1) in general, non-salmonid fishes would consume terrestrial food items to the same extent as salmonids; and (2) subsidy consumption would be associated with jaw morphology. Cyprinids and fundulids consumed terrestrial subsidies approaching levels observed in salmonids (20–44%) whereas other groups (e.g. catostomids and moronids) consumed far less (<2%) terrestrial food. Fishes with terminal jaw positions tended to consume more terrestrial items than those with subterminal or inferior jaw positions. Within a species, there were highly variable propensities for consuming terrestrial subsidies. Our findings justify focusing on trophic linkages between fishes and riparian systems across a wide range of taxa, especially considering the spatio-temporal variability of environmental conditions across a variety of habitats. It is necessary to assess the relative contribution of terrestrial subsidies in fish growth and population dynamics with a focus on nutritional and energetic benefits across different groups.

Additional keywords: allochthony, fish foraging, jaw position, subsidies, terrestrial prey.

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Introduction

The intimate relationship between stream ecosystems and the adjacent terrestrial riparian zones has long been recognised (Minshall 1967; Likens and Bormann 1974). Although terrestrial leaf litter provides the energy basis for many stream systems, terrestrial arthropods can also subsidise aquatic consumers, especially fishes. The flow of energy between ecosystems might be affected by the relative availability of *in situ* prey items versus the subsidy (Marczak *et al.* 2007), but it can also be related to the relative productivity values of donor and recipient ecosystems (Polis *et al.* 1997; Zhang *et al.* 2003). Patterns in such subsidy mediation of energy flow may be better understood by assessing the contributions of terrestrial subsidies to fish diets across taxa and geographic regions.

Empirical studies on fish foraging indicate that the consumption of terrestrial subsidies by fishes (Balcombe *et al.* 2005; Bojsen 2005) is a global phenomenon, with ecosystem-level relevance for food web and community dynamics (Baxter *et al.* 2005). There is increasing evidence that fishes consuming terrestrial seeds may be important seed dispersers in both temperate and tropical systems (Horn 1997; Horn *et al.* 2011). One family of fishes, Salmonidae, appears to consume terrestrial food items with a greater consistency than other fishes. Terrestrial subsidies constituted 68% of the diet of coho salmon (*Oncorhynchus kisutch*) (Eberle and Stanford 2009) and contributed over 50% of a salmonid species' annual energy budget (Nakano and Murakami 2001; Utz and Hartman 2007). In other cases, salmonids consume only moderate amounts of terrestrial subsidies (10–20%, Thomas 1962; Tippets and Moyle 1978; Cada *et al.* 1987).

To assess general taxonomic and morphological patterns of the consumption of terrestrial foods by fishes, we used published values of percentages of terrestrial subsidy contributions to fish diets. Owing to the great taxonomic and geographic variability of fish communities, we restricted our analysis to the USA. Outside of salmonid-dominated systems, little work has been done on fish communities, which explicitly focuses on the importance of terrestrial food in streams in the USA (cf. Cloe and Garman 1996). We did not set out *a priori* to test if other fish species consume more or fewer terrestrial food items than salmonids, but we did expect that terrestrial subsidy inputs would be important for many fish taxa outside of ecosystems where salmonids evolved.

We analysed several fish families (Catostomidae, Centrarchidae, Cottidae, Cyprinidae, Fundulidae, Ictaluridae, Moronidae and Percidae) to determine which, if any, tend to utilise more terrestrial subsidy inputs and to what extent. We predicted that if there were families that tended to consume terrestrial food items more than others, there would be an association with that family's jaw position (e.g. inferior, subterminal and terminal jaw types). Since terrestrial subsidy inputs must enter the aquatic system from the water's surface, we predicted that fishes with more upturned jaw positions (i.e. terminal) would consume more terrestrial items than those with more downward-opening mouths. Jaw morphology has been shown to be an important factor in the sizes and types of prey that fishes consume (Hugueny and Pouilly 1999; Keeley and Grant 2001). We also assessed patterns in the types of terrestrial food items consumed by fishes. This is an important component because understanding the particular types of prey items that fishes consume can guide more exacting riparian management strategies.

Materials and methods

We used empirical data from 37 published studies representing 55 fish species and 74 total diet observations from the USA (see Table S1/Fig. S1, available as Supplementary Material to this paper) to examine the pattern of the percentage of terrestrial food items in fish diet. We restricted our analyses to this geographic region because both taxonomic and environmental variability makes broad comparisons of diet difficult. However, this study encompasses a large geographic range within the USA. The percentage contribution of terrestrial food items was used as a response variable, averaged across seasons or size classes, depending on which way the data were presented. In cases where the authors reported both, we opted for a mean across seasons to capture temporal variability. We recorded only explicitly identified terrestrial food items. For example, if the original reference combined winged-adult aquatic insects with terrestrial food items, those observations were discarded. The category of 'terrestrial food items', therefore, includes both plant and animal remains but the majority of the terrestrial diet remains are of arthropods. The dataset that we obtained was primarily represented by diets of fishes in lotic systems. Five of the 37 published studies analysed represented diets of fishes collected in lentic systems, all of which were reservoirs.

For each study, our database was populated using both environmental and biological variables. We used fish species (for original papers that include multiple species, each species was entered as an independent observation) and fish family. We categorised each species based on jaw morphology (inferior, subterminal and terminal) from Barton (2006) and Goldstein and Simon (1999). Superior mouth positions were not included as none of the species analysed possess this mouth configuration. This was determined by species accounts in Pflieger (1997), Etnier and Starnes (2001) and Thomas *et al.* (2007). We accepted three quantitative diet methods for our analyses that were categorised and interpreted using Hyslop (1980).

(1) Percentage by abundance of food items (PBA), calculated as the total number of a particular prey items over the grand total number of prey items ingested by fish.
(2) Percentage by mass of food items (PBM), calculated as the mass of a particular prey category over the total mass of all prey items ingested by fish. This method is most often expressed as dry weight in grams or milligrams.
(3) Percentage by volume of food items (PBV), which is similar to PBM but uses volume displacement instead of weight. A prey category is placed into a graduated container with liquid and the net volume is recorded. The percentage is the composition (%) of food items over the grand total of displacement in fish stomach contents for all food categories.

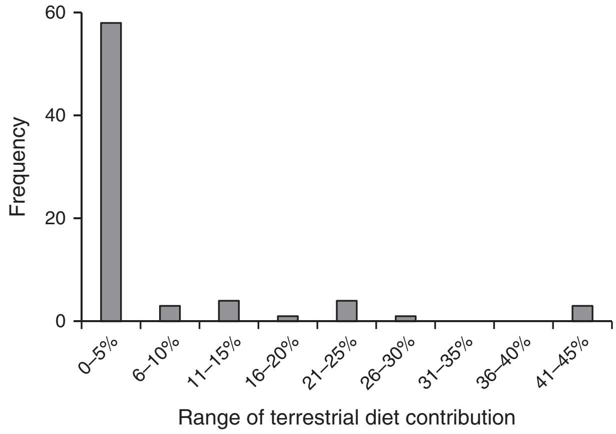

Fig. 1. Frequency distribution of fish diet observations ($n = 74$) across ranges of % terrestrial contribution to diet.

Owing to the high variability and sensitivity to food abundance, we did not use percentage by occurrence or frequency of occurrence.

Results

Across all diet composition metrics (i.e. abundance, mass, volume), terrestrial subsidies occurred among representative taxa in five of the eight families (63%) and 37 of the 55 species (68%) surveyed in this study. Percentage contributions of terrestrial subsidies ranged from 0% among representative taxa of three families (Catostomidae, Cottidae and Moronidae) to 41% among fundulids and 44% among cyprinids. Terrestrial subsidies were rare in percids (<1%), centrarchids (5%) and ictalurids (up to 13%). Among species and reported diets ($n = 74$), terrestrial food items were absent to rare (0–15% contribution) in 88% ($n = 65$) of observations, moderate (16–30%) in 8% ($n = 6$) of observations and high (30–44%) in 4% ($n = 4$) of observations (Fig. 1). Of the studies that explicitly identified terrestrial subsidy taxa ($n = 20$ studies and $n = 34$ diet observations), hymenopterans were the most frequent terrestrial subsidy across diet methods, occurring in 30 (88%) of observations. Coleopterans occurred in 59%, orthopterans in 32% and plant materials occurred in 41%. Cyprinids consumed all terrestrial subsidy types identified, hymenopterans being the most frequent, occurring in 25 (93%) of the 27 cyprinid diet observations (Table 1).

The percentages of terrestrial subsidies in fish diets were greatest in small-bodied cyprinids and fundulids. Mean percentage volume of terrestrial subsidies was 15% (range: 1–44%) among three cyprinid genera and 14 species (Table 2). Mean percentage volume was 33% (range: 22–41%; $n = 2$) in *Luxilus* diets, 18% (range: 2–44%; $n = 4$) in *Cyprinella* diets and 9.5% (range: 1–23%; $n = 8$) in *Notropis* diets (Table 3). All of the studies ($n = 7$) where cyprinids consumed moderate to high (>20%) terrestrial subsidies were sampled from stream systems with dense forest cover in portions of the sampling reach, suggesting a relationship between terrestrial subsidy availability and habitat. However, there were also instances where cyprinids within the same forested stream consumed little or no terrestrial

Table 1. Frequency of terrestrial subsidy categories within fish families and diet method for the studies that specifically identified terrestrial remains

($n = 20$ studies and $n = 34$ diet observations). Note that species within families consume multiple terrestrial subsidy types. PBA, percentage by abundance; PBM, percentage by mass; PBV, percentage by volume

	Terrestrial subsidy category			
	Hymenoptera	Coleoptera	Orthoptera	Seeds/Plant material
Centrarchidae	3	1	0	0
PBA	1	0	0	0
PBM	1	1	0	0
PBV	1	0	0	0
Cyprinidae	25	18	11	11
PBA	5	2	1	1
PBM	5	3	2	0
PBV	15	13	8	10
Fundulidae	1	0	0	2
PBV	1	0	0	2
Ictaluridae	1	1	0	1
PBA	1	1	0	1
Grand total	30	20	11	14

Table 2. Summary of the range of percentages of terrestrial subsidy contribution for each family analysed

Cell values are ranges and the number of observations for each cell (in parentheses) is given for each diet method. PBA, percentage by abundance of food items; PBM, percentage by mass of food items; PBV, percentage by volume of food items

	Diet technique		
	PBA	PBM	PBV
Catostomidae	0.0–0.0 (1)	0.0–0.0 (2)	0.0–0.0 (1)
Centrarchidae	0.0–4.1 (6)	2.3–5.3 (3)	0.7–2.2 (3)
Cottidae	0.0–0.0 (2)	–	–
Cyprinidae	0.0–15.0 (8)	0.3–7.2 (6)	0.0–44.0 (25)
Fundulidae	–	–	1.0–40.8 (3)
Ictaluridae	0.0–3.8 (4)	0.0–13.0 (2)	0.0–0.0 (1)
Moronidae	–	0.0–0.0 (1)	0.0–0.0 (1)
Percidae	0.0–1.0 (5)	–	–

items. Mean percentage volume was 15% (range: 1–41%) among three species of fundulids. No habitat-mediated variability in terrestrial diet contribution for fundulids could be ascertained; all three species were sampled from lentic systems and only *Fundulus notatus* was observed to consume a high amount of terrestrial food (41%).

Terrestrial subsidy abundance was relatively low but terrestrial items were consistently consumed among species of one of the most popular non-salmonid sport fish genera (*Micropterus*). Mean percentage terrestrial subsidies were 1% (range: 1–2%) by volume for *M. dolomieu*, *M. punctulatus* and *M. salmoides* and 3% (range: 2–3%) by percentage biomass for (*M. dolomieu* and *M. salmoides*). Seasonally, percentage contributions were highest in spring for both *M. dolomieu* (4%) and in *M. salmoides* (7%). Among studies, micropterids were primarily sampled from streams, but the greatest average terrestrial subsidies were observed (4% by abundance) from lentic habitats.

Table 3. Summary of the mean percentages of terrestrial subsidy contribution to fish diet for each family and diet method

Cell values represent mean terrestrial contribution to diet (%) and standard deviations are in parentheses. PBA, percentage by abundance of food items; PBM, percentage by mass of food items; PBV, percentage by volume of food items

Fish family	Diet method		
	PBA ($n = 26$)	PBM ($n = 14$)	PBV ($n = 34$)
Catostomidae ($n = 4$)	0.0	0.0	0.0
Centrarchidae ($n = 7$)	1.1 (1.7)	3.6 (1.5)	1.4 (0.8)
Cottidae ($n = 1$)	0.0	–	–
Cyprinidae ($n = 29$)	4.7 (6.3)	3.9 (2.5)	10.8 (13.3)
Fundulidae ($n = 3$)	–	–	14.7 (22.6)
Ictaluridae ($n = 5$)	1.3 (1.7)	6.5 (9.2)	0.0
Moronidae ($n = 1$)	–	0.0	0.0
Percidae ($n = 5$)	0.3 (0.5)	–	–

Table 4. Summary of data analysed for jaw positions inferior, subterminal and terminal

The mean percentages of terrestrial contribution to diet are given along with sample sizes for each jaw position and diet technique category (samples sizes are in parentheses). Range % TI column represents the range of percentages of terrestrial inputs observed within each jaw morphology category. PBA, percentage by abundance of food items; PBM, percentage by mass of food items; PBV, percentage by volume of food items

Jaw orientation	PBA	PBM	PBV	Total N	Range % TI
Inferior	0.0 (1)	0.2 (2)	2.3 (3)	6	0.0–6.8
Subterminal	0.9 (8)	4.2 (6)	2.0 (7)	21	0.0–13.0
Terminal	2.5 (17)	3.7 (6)	12.4 (24)	47	0.0–44.0

Terrestrial food items were reported in the diets of fish with inferior, subterminal and terminal jaw positions. Across categories of diet techniques, mean percentage terrestrial subsidies in the diets were lowest in fishes with inferior jaw positions and highest in fishes with terminal jaw positions (Table 4). Maximum percentage terrestrial subsidies in fish diets were 7% for inferior, 13% for subterminal and 44% for terminal jaw positions. Greatest familial diversity of jaw morphology was observed within cyprinids, which were represented by all three jaw positions. Among cyprinids, mean percentage volumes of terrestrial subsidies were 2% ($n = 3$ observations) for inferior jaw positions, 2% ($n = 7$) for subterminal jaw positions and 12% ($n = 24$) for terminal positions.

Discussion

Terrestrial food subsidies frequently occurred within the diets of fishes (68%) reviewed in this study and had moderate to high (11–44%) contributions in 12% of the fishes. Greater terrestrial food subsidies were associated with smaller-bodied fishes and fishes with terminal jaw positions and the input of terrestrial invertebrates was greatest in stream segments with dense vegetation cover along the stream margin. In general, the percentage contribution of terrestrial food subsidies was lower (<45%) in non-salmonid stream fishes, although percentage contributions for some species of Cyprinidae and Fundulidae approached those levels observed in the Salmonidae. Salmonids from stream habitats consume >50% terrestrial subsidies (Wipfli 1997; Eberle and Stanford 2009; Rosenfeld and Raeburn 2009), attributed to competition or low productivity of salmonid streams.

Large amounts of terrestrial subsidies in the diets of salmonids, especially larger conspecifics, are also partly attributed to interspecific and intraspecific competition (Nakano 1995). Salmonids in stream habitats display hierarchical feeding behaviour, where larger individuals are more likely to occupy focal feeding spaces that have more optimal water velocities and better access to drifting invertebrates (Fausch and White 1981; Sabo and Pauley 1997), suggesting that larger salmonids will consume a greater amount of terrestrial food as well. We were unable to test the effects of size and amount of terrestrial food consumed within species (e.g. intraspecific competition). However, interspecific competition is unlikely to influence which non-salmonid family will consume large amounts of terrestrial subsidies, given that the smaller-bodied cyprinids and fundulids had the highest percentage contribution of terrestrial subsidies. In fact, length of fish as a predictor of the amount of terrestrial subsidies is not consistent among salmonids. Coho salmon (40–180 mm fork length) consumed similar amounts of terrestrial food items (40–60%) across several study sites (Wipfli 1997; Eberle and Stanford 2009; Rosenfeld and Raeburn 2009). Native Dolly Varden charr (*Salvelinus malma*) were empirically shown to be inferior competitors for terrestrial and drifting food items when compared with similarly sized, introduced rainbow trout (Baxter *et al.* 2007). Intermediate sizes (70–120 mm) of brown trout (*Salmo trutta*) consumed greater amounts of terrestrial food (23%) than smaller (<70 mm) or larger (>120 mm) individuals with 5 and 18% terrestrial food contributions to diet respectively (Elliott 1967).

Large amounts of terrestrial subsidies in the diets of salmonids also are attributed in part to low instream productivity. The importance of a trophic subsidy can be mediated by the relative productivities of the adjacent systems, as conceptualised by Polis and Hurd (1996) and further explored by Marczak *et al.* (2007) and Paetzold *et al.* (2008). In general, macroinvertebrates in tropical and subtropical streams generally have greater in-stream secondary productivity (Benke and Jacobi 1986; Huryn and Wallace 2000) and obtain greater body mass (Morin 1997) than macroinvertebrates in relatively cold streams (Allen 1951). This suggests that *in situ* energy limitation in cold-water systems may be driving the reliance upon terrestrial food subsidies observed among salmonids. Stream fish communities in warmer waters, especially in the south-eastern USA might rely less upon terrestrial food subsidies because of greater in-stream productivity due to relatively warm annual temperatures.

Fishes in biographical regions outside of the neartic region of North America consume high amounts of terrestrial subsidies seasonally and year-round. Terrestrial food subsidies range from 35% in a cyprinid within subtropical regions of Asia (Chan *et al.* 2008) to 70% among several characin species in Ecuador (Bojsen 2005). Bojsen (2005) found that the consumption of terrestrial food subsidies was particularly great, ranging between 65 and 71%. Stream fishes in Australia have also been observed to consume considerable amounts of terrestrial food subsidy (Balcombe *et al.* 2005; Davis *et al.* 2010), especially *Melanotaenia splendida tatei* (Melanotaeniidae), which was observed to consume an average of 66% terrestrial food items (Balcombe *et al.* 2005). Consumption of terrestrial items can be higher during the monsoon season by a native retropinnid in Australia (Balcombe *et al.* 2005) and year-round by a galaxid at higher latitudes of New Zealand (West *et al.* 2005). Fruit and seed-eating fishes are most abundant within tropical regions of South America with some small-bodied characin and cichlid species consuming fruits and seeds seasonally and opportunistically along with other aquatic and terrestrial invertebrates, whereas some larger-bodied and herbivorous fishes can consume fruits and seeds either opportunistically or preferentially (Horn *et al.* 2011). Horn *et al.* (2011) suggested that specialisation on terrestrial subsidies by the larger-bodied herbivorous fishes might be adaptive based on the evolutionary history and diverse lineages of fruit-eating fishes within the long-persisting tropical rainforests of South America.

Collectively, salmonids and fishes in tropical regions consumed higher amounts of terrestrial subsidies than the majority (88%) of the non-salmonid stream fishes surveyed in this study that consumed <15% of terrestrial inputs. Lower consumption of terrestrial food subsidies outside of salmonid streams of the USA is attributed to two plausible mechanisms. First, antiquity of the land–water flora and fauna communities in the tropics likely provided longer and more persistent biotic and abiotic interactions, allowing fishes to specialise on available terrestrial nutrient sources (Horn *et al.* 2011). Plants and animal communities of higher latitudes (i.e. temperate and subtropical regions) are more variable because they have been more heavily influenced by cyclic warm/cold climates during the last 2 million years. Radiations within fish communities of specialised consumers of terrestrial food may be inhibited because the land–water communities changed substantially with each advancing and retreating glacial event. This mechanism, described by Horn *et al.* (2011) to explain the high occurrence of fruit- and seed-eating fishes in the tropics of South American, offers an explanation on why terrestrial subsidies comprised a greater proportion of the diets in tropical fishes versus temperate fishes, but the patterns were not consistent with high frequency and abundance of terrestrial subsidies in the diets of salmonids at higher latitude of North America. A second, smaller-scale mechanism might be operating within areas of glacial influence and regulated by the relative productivities of stream and adjacent riparian communities. Within the USA, cooler and more temperate streams where salmonids live are relatively less productive than the warmer streams in the subtropical regions. Therefore, our observation that fishes in warmer, more subtropical streams rely less upon terrestrial food subsidies than salmonids in higher latitudes might reflect a smaller differential between the productivity within the stream and the adjacent riparian area.

Regardless of the relatively low biomass, volume and abundance of terrestrial inputs, non-salmonid stream fishes of the USA frequently consumed at least some terrestrial subsidies and at times, these comprised high proportions of the total diet.

Terrestrial invertebrate inputs to forest stream ecosystems often represent both high quality and high quantity food source as an important trophic link between riparian zones and stream food webs (Mason and MacDonald 1982; Allan *et al.* 2003; Francis and Schindler 2009). This suggests that terrestrial inputs, independent of the amount, are important in the survival, growth and productivity of the fish communities or simply opportunistic feeding by highly voracious, non-selective, drift-feeding invertivores (Goldstein and Simon 1999). Even among salmonids, linkages between terrestrial subsidies and health of the fish community remain unclear with respect to the abundance and productivity of fishes (Baxter *et al.* 2005; Zhang and Richardson 2011). Nakano and Murakami (2001) estimated the mean annual energetic contribution of terrestrial food subsidy to a stream fish community in a forested Japanese stream to equal 44%, but this ranged from 12 to 57% depending on species. Among the five species examined, four were salmonids and the fifth was a sculpin (Cottidae) which consumed the lowest amount of terrestrial food. Growth rates of Dolly Varden charr decreased by 31% when terrestrial subsidies were experimentally excluded from their diets, but Kawaguchi *et al.* (2003) found no detectable change growth rates among salmonid species with similar experimental exclusions. Using a bioenergetics model, Sweka and Hartman (2008) predicted that a 25% annual reduction in the terrestrial subsidies into a stream would reduce growth of brook trout (*Salvelinus fontinalis*) by ~25%. Additional experimental manipulations on fish growth are necessary, especially outside of salmonid communities, to determine if terrestrial subsidies are necessary and selectively sought among some members of the fish community or are simply an opportunistic feeding event with little regulating role of the aquatic community. From a management perspective, understanding the role of terrestrial subsidies in the nutrient uptake of stream fishes will identify additional benefits of intact watershed and riparian vegetation cover to the biotic community of streams.

The importance of intact riparian areas to stream ecosystem structure and functioning is well known for provision of shading for temperature mitigation and of woody debris and undercut banks for refugia, buffering sediments and trapping nutrients and contaminants (Naiman and Décamps 1997; Pusey and Arthington 2003; Whitledge *et al.* 2006). Although the specific role of riparian zones in providing food resources for stream fishes outside of salmonid communities has not been assessed to the same extent (but see Garman 1991 and Cloe and Garman1996), our results indicate that more research is needed to explore the importance of terrestrial food subsidy for fish population dynamics across a wide variety of taxa and regions. In general, the consumption of terrestrial food items by fishes is highly variable, so it will be necessary to address the importance of terrestrial subsidies in a particular system on a case by case basis with consideration of spatial and temporal variation in subsidy availability.

The question of how important terrestrial food subsidy is for non-salmonid fishes from an energetic standpoint still remains unanswered. Terrestrial food subsidies were estimated to be more energy-rich on a per gram basis than aquatic food items (Francis and Schindler 2009). If this is true as a generality, terrestrial food subsidies might contribute greatly to a fish's energy budget, even at a low relative contribution, especially during a season with the low biomass availability of benthic macroinvertebrates (Cloe and Garman 1996; Nakano and Murakami 2001). Thus, our study provides support to justify further research into the estimation of the energetic contribution of terrestrial food subsidies to stream fish communities, considering the spatio-temporal variability of environmental conditions across a variety of ecoregions. Such subsidy contribution may provide ubiquitous and significant terrestrial–aquatic energetic linkages for fishes worldwide.

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