

The effects of riparian disturbance on the condition and summer diets of age-0 brook trout (*Salvelinus fontinalis*) in three central Appalachian streams

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Abstract: Forested headwater streams are dependent on their riparian zones for many critical goods and services. It is assumed that riparian disturbance affects stream food webs, but for some ecologically and economically important taxa like brook trout (*Salvelinus fontinalis*), little research has been performed. This study found that intense but spatially limited riparian disturbance resulted in significant but context-dependent changes in the diets and condition of age-0 brook trout in three central Appalachian streams. Dietary shifts in two of the streams appeared to enable age-0 brook trout to maintain or increase condition following riparian tree removal. A significant relationship between fish condition and the importance of Ephemeroptera as prey was observed. The lack of dietary shift to energetically important ephemeropterans coincided with decreased fish condition within one stream previously identified to be mildly impacted by acid precipitation. The context within which riparian disturbance occurs plays an important role in determining the overall impact to age-0 brook trout and should be an important consideration in future regulatory and management decisions.

Résumé : Les cours d'eau d'amont en milieu boisé dépendent de leurs zones riveraines pour de nombreux biens et services clés. S'il est généralement tenu pour acquis que la perturbation des zones riveraines à une incidence sur les réseaux trophiques des cours d'eau, peu de travaux ont visé certains taxons d'importance écologique et économique comme l'omble de fontaine (*Salvelinus fontinalis*). Nous avons constaté que des perturbations intenses, mais limitées dans l'espace se traduisaient par des modifications significatives, mais dépendantes du contexte des régimes alimentaires et de l'embonpoint d'ombles de fontaine de moins de 1 an dans trois cours d'eau du centre des Appalaches. Les modifications du régime alimentaire dans deux des cours d'eau semblaient permettre aux ombles de fontaine de moins de 1 an de maintenir ou d'accroître leur embonpoint après le retrait d'arbres dans la zone riveraine. Une relation significative entre l'embonpoint des poissons et l'importance des éphéméroptères comme proies a été observée. L'absence d'un changement du régime alimentaire vers des éphéméroptères importants sur le plan énergétique coïncidait avec une diminution de l'embonpoint des poissons dans un cours d'eau dans lequel des impacts modérés de précipitations acides avaient déjà été décelés. Le contexte dans lequel les perturbations des zones riveraines se produisent joue un rôle important dans la détermination de l'impact global sur les ombles de fontaine de moins de 1 an dont il importe de tenir compte dans les décisions futures touchant à la réglementation et la gestion. [Traduit par la Rédaction]

Introduction

Brook trout (*Salvelinus fontinalis*) are the only salmonids native to central Appalachia and are ecologically and economically important, as they support a recreational fishery and are often the largest aquatic predator in these systems. Unfortunately, human activities have caused brook trout populations to decrease across most of their range (EBTJV 2006). Within West Virginia, poor land management, logging practices, acid deposition, and acid mine drainage are the main threats to brook trout (EBTJV 2006). The cool headwater streams that brook trout inhabit have particularly strong interactions with their riparian zones and may be especially susceptible to riparian disturbance (Nakano and Murakami 2001; Baxter et al. 2005).

Streams rely on riparian zones for many critical goods and services. The riparian interface regulates stream temperature (Hetrick et al. 1998; Moore et al. 2005), functions as a filter, buffer, and stabilizer (Keller and Swanson 1979; Naiman and Decamps 1997), and is the source of in-stream large woody debris. The services and products of riparian areas can be altered by disturbances such as timber harvest (Davies and Nelson 1994), development (Sponseller et al. 2008), windthrow (Grizzel and Wolff 1998), fire (Minshall 2003), and arboreal disease (Swanston 1991). Disturbance plays a key role in stream ecology, and experimental studies are required to increase our understanding of these complex systems (Resh et al. 1988).

Riparian disturbance often decreases canopy cover, which leads to increased solar radiation and higher stream temperatures (Studinski et al. 2012). Warmer streams impose greater metabolic demands on brook trout (Hartman and Cox 2008), which typically occupy low-productivity systems and often feed at or near maintenance ration (Sweka and Hartman 2001; Utz and Hartman 2006). Age-0 brook trout are likely to be more sensitive to habitat disruption than adults due to their limited energy reserves and lower capacity for dispersal (Hunt 1969; Ware 1978; Ensign et al. 1990;

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Fig. 1. Location and watersheds of the three study streams in eastern West Virginia, USA. The watersheds' most downstream point represents the downstream boundary of the disturbed reaches. [Color online.]



Biro et al. 2004), making relocation a proportionally costlier activity when compared to adult brook trout. Age-0 brook trout must grow quickly to escape predation and defend territories, and therefore, small changes in available energy could have magnified implications for their survival (Cunjak et al. 1987).

In addition to higher stream temperatures, a reduction of riparian canopy cover may alter the allochthonous and autochthonous energy sources for age-0 brook trout. A reduced canopy often results in increases in the biomass of algae and scrapers (Wallace and Gurtz 1986; Stone and Wallace 1998; Kiffney et al. 2003). Riparian disturbance has also been shown to increase terrestrial invertebrate biomass (Brown 1984) and alter the composition of terrestrial invertebrates entering the stream (Studinski and Hartman 2014), which are an important food source for adult brook trout (Kawaguchi and Nakano 2001; Utz and Hartman 2007). The importance of terrestrial invertebrates as an energy source for age-0 brook trout is unknown, and little research has been performed on the diets of age-0 brook trout (Walsh et al. 1988 (Quebec); Fechney 1988 (New Zealand)) or the effects of small-scale riparian disturbance on their condition (Wilson et al. 2014). Therefore, the objectives of this study were to determine if riparian disturbance affects the summer diets and condition of age-0 brook trout in three central Appalachian streams.

Material and methods

Study sites and experimental design

This study was conducted in three tributaries of the Middle Fork River, Randolph County, West Virginia, USA (Fig. 1). The watershed is located in the Allegheny Plateau physiographic province in central Appalachia. Rocky Run, Mitchell Lick, and Schoolcraft Run are first- or second-order streams and are at elevations of 724-808 m (Fig. 1; Table 1). The streams occasionally experience periods of low flow or no flow during summer. The streams are surrounded by a mixed mesophytic forest (Van Sambeek et al. 2003), which was owned and managed for saw timber and fiber production by MeadWestvaco Corporation but was sold to Penn-Virginia Corporation during the study. The riparian forest is 70-85 years old and is dominated by black birch (Betula lenta), sugar maple (Acer saccharum), yellow birch (Betula alleghaniensis), and yellow poplar (Liriodendron tulipifera). The forest has a basal area of approximately 27.5 m²/ha. The experimental streams flowed over poorly buffered Pottsville geology and have had limestone sand added annually since the mid-1990s by the West Virginia Department of Natural Resources to mitigate the effects of acid precipitation. All streams contain resident brook trout populations and, typical of Appalachian headwater streams, fish species diversity is low. Brook trout are the dominant species, with mottled sculpin (Cottus bairdii), creek chub (Semotilus atromaculatus), and blacknose dace (Rhinichthys atratulus) also present.

Two 250 m long study reaches, hereafter "disturbed" and "reference" sections, were established on each stream. To isolate the effects of the treatment, the reference section was placed upstream of the disturbed section in each stream, and the two reaches were separated by 100 m of stream with an undisturbed riparian area. The riparian zone of the disturbed section of each stream was subjected to a 90% basal area removal timber harvest that extended perpendicularly 30 m from each stream bank. Riparian tree removal began in July 2006 and was completed in December 2007. During the timber harvest, any large woody debris that fell into the stream channel was removed.

Data collection

Brook trout were sampled in both reaches of each of the three streams on 21 June 2010, 27 July 2010, 16 August 2010, and 24 September 2010 using a pulsed DC backpack electrofishing unit and a two-pass removal technique. These dates encompass the period of peak terrestrial invertebrate consumption by stream salmonids (Wipfli 1997; Kawaguchi and Nakano 2001; Utz and Hartman 2007; Sweka and Hartman 2008). A target sample size of 30 age-0 brook trout was used for each stream reach in each of the four months. Fish were anesthetized in a 120 mg/L solution of clove oil (Anderson et al. 1997), individually weighed to the nearest 0.01 g, and measured to the nearest millimetre total length. Stomach contents were removed via gastric lavage, where a constant flow of stream water was directed into the foregut until all items had been apparently collected. This process has been shown to be a nonlethal and effective method in removing all stomach contents from age-0 brook trout (Hafs et al. 2011). Gut items were filtered with a 250 μm sieve and transferred to 95% ethanol. Fish were released back into the area of capture following the fish processing procedures. All field methods were approved by the West Virginia University Institutional Animal Care and Use Committee using protocol No. 09-0404.

In the laboratory, prey items were identified to family when possible, although large, soft-bodied taxa like Lepidoptera larvae were often identifiable only to order. The length of each prey item was recorded so that dry mass could be estimated from published length–weight regressions (Schoener 1980; Sage 1982; Sample et al. 1993; Benke et al. 1999; Sabo et al. 2002). The life stage (larvae or adult) and habitat (terrestrial or aquatic) of each prey item were also recorded.

Data analysis

A percent index of relative importance (%IRI) score, which is a standardized index of relative importance, was calculated for each taxa. %IRI takes into consideration abundance, mass, and occurrence among samples and has been shown to be a robust and

Table 1. Abiot	tic attributes of three	central Appa	lachian streams.
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	Treatment	Daily stream maximum (°C)	Stream – ambient (°C)	Watershed size (ha)	Slope (%)	pН
Mitchell Lick	Disturbed	19.4	-4.7	226	3.7	6.7
	Reference	15.7	-8.3			
Rocky Run	Disturbed	17.2	-6.4	750	3.3	5.4
0	Reference	15.3	-8.4			
Schoolcraft Run	Disturbed	20.4	-3.2	759	2.8	6.7
	Reference	15.6	-8.0			

Note: Stream pH values are from Studinski (2010) and stream temperature values are summarized from Studinski et al. (2012). Temperature and pH data were collected 2 years prior to collection of age-0 brook trout diets. Temperature data were collected during summer, but not simultaneously, so stream temperature minus ambient air temperature values are included.

balanced IRI (Liao et al. 2001). Due to the degradation of some soft-bodied taxa, %IRI scores were calculated at the rank of order, with distinctions made between life stage and habitat. Using the order-level %IRI scores, changes in the composition of age-0 brook trout diets due to disturbance, month, and stream were analyzed using a nonparametric permutational multivariate analysis of variance (ANOVA) (PerMANOVA). Data were ln(x + 1) transformed, and the analysis was based on Bray-Curtis dissimilarities. Permutation of residuals occurred under the reduced model, with 9999 permutations used for each test.

Fish condition was calculated as relative condition (LeCren 1951) after the weight of prey was removed. To determine which factors explained a significant portion of the variation in fish condition, the Akaike information criterion (AIC) was used to select the best supported regression model out of the suite of all possible model combinations including treatment, stream, or month and all second-order interactions (Akaike 1973). A multifactor ANOVA with post-hoc Tukey HSD tests was used to identify significant differences in fish condition between levels of the main factors identified by AIC to be well supported. An additional multifactor ANOVA was used to investigate any effects of stream, month, or treatment on the total mass of the diet samples.

Fish density for each section and time period was determined by using the general weighted *k*-pass estimator proposed by Carle and Strub (1978) and was compared to median fish condition of the section using basic regression techniques. Program R (R Core Team 2015) was used for all analyses except for the PerMANOVA, which was performed with PERMANOVA (Anderson 2005).

Results

A total of 6150 diet items representing 118 taxa were collected from 663 age-0 brook trout. Prey habitat (terrestrial or aquatic) was balanced in reference sections, with the %IRI scores of aquatic and terrestrial prey of 48.4 and 51.6, respectively. In disturbed sections, a shift toward aquatic prey was observed, with %IRI scores of 66.0 for aquatic prey and 34.0 for terrestrial prey. Across all reaches, by dry mass, invertebrates made up 96% of prey items consumed, with the remaining 4% being vertebrates in the Cottidae and Plethodontidae families. Ephemeroptera larvae, terrestrial adult dipterans, and aquatic larval dipterans were common across both treatments, while terrestrial lepidopteran larvae and terrestrial dipteran larvae (mainly Cecidomyiidae, gall midges) were better represented in fish diets from reference sections (Table 2). The PerMANOVA revealed that fish diet composition varied by treatment (p = 0.006, Df = 1, F = 2.64), month (*p* = <0.001, df = 3, *F* = 4.40), and stream (*p* = 0.014, df = 2, *F* = 1.98). Post-hoc comparisons investigating the effects of disturbance indicated significant changes in the composition of age-0 brook trout diets in both Mitchell Lick (p = 0.034, t = 1.63) and Schoolcraft Run (p = 0.031, t = 1.92) but not in Rocky Run (p = 0.806, t = 0.87).

Brook trout condition was affected by treatment, stream, and month (Fig. 2; Tables 3 and 4). From the suite of candidate models that predicted brook trout condition, the best supported model included all possible factors and interactions (condition = treatment + month + stream + treatment × month + treatment × stream + month × stream; AIC = -1237.106) (Table 3). This suggests that stream, month, and treatment all had a significant influence on age-0 brook trout condition (Table 4). Similarly, the multifactor ANOVA indicated that all three main effects significantly affected condition (treatment: p = 0.0497, df = 1, F = 3.87; month: p = 0.024, df = 3, F = 3.168; stream: p = 0.043, df = 2, F = 3.16). Post-hoc analyses (Fig. 2) indicated that when compared to the corresponding reference section, riparian disturbance was associated with a decrease in fish condition in Rocky Run (p = 0.028, df = 1, F = 4.92), an increase in fish condition in Schoolcraft Run (p < 0.001, df = 1, F =24.69), and no change in fish condition in Mitchell Lick (p = 0.799, df = 1, F = 0.06).

The mass of stomach contents per fish (milligrams dry weight) was affected by stream (p < 0.001, df = 2, F = 10.44) and month (p < 0.001, df = 3, F = 5.64) but not treatment (p = 0.547, df = 1, F = 0.36). Age-0 brook trout density varied among streams (Table 5) but was not significantly related to median fish condition (p = 0.50, $R^2 = 0.02$). Due to the apparent importance of larval Ephemeroptera as prey, median fish condition was compared to the %IRI score for larval Ephemeroptera using nonlinear least squares analysis. A nonlinear relationship was observed (Fig. 3), where predicted and observed condition values were significantly related (p < 0.01, $R^2 = 0.44$).

Discussion

Similar to adult brook trout, age-0 fish rely heavily on terrestrial invertebrates as an energy source during summer months, especially under reference conditions (Table 2). Previous research, some of which occurred on these same streams, suggests that recently disturbed riparian areas may contain and donate a greater biomass of terrestrial invertebrates to streams (Allan et al. 2003; Studinski and Hartman 2014), but adult brook trout in those reaches appear to shift their diets towards aquatic prey (Niles 2010; Wilson et al. 2014). Similarly, the age-0 brook trout in this study shifted their diets towards aquatic prey in disturbed reaches, suggesting that in-stream invertebrate availability affects prey choice.

The response of diets and condition of age-0 brook trout to riparian disturbance was not consistent, despite the three streams being superficially similar and located within a few kilometres of each other (Fig. 1). The pH varies among the three streams (Table 1) and likely contributes to the incongruent findings in the more acidic Rocky Run via reduced invertebrate productivity. Other factors, such as differences in density-dependent effects, stream flow, temperature, sedimentation, and periphyton productivity, do not explain the varied response of age-0 brook trout condition to disturbance in these streams (Table 5). Density-dependent effects have been shown to affect the response of fish condition to riparian disturbance (Xu et al. 2010), but in this study, fish condition was not related to fish density. Low summertime stream flow can exacerbate the trophic response to disturbance and decrease

Table 2.	Fish	condition	and %	%IRI s	scores	(pooled	across	months)	for the	10	highest	scoring	taxa l	by '	treatment	and
stream.																

Таха	Life stage	Habitat	%IRI score	Таха	Life stage	Habitat	%IRI score	
Mitchell Lick, dis	turbed section	n, meduan fis	h	Mitchell Lick, refe	erence section	n, median fish		
condition: 0.99	0			condition: 0.98	5			
Ephemeroptera	Larvae	Aquatic	45.9	Diptera	Larvae	Aquatic	43.7	
Diptera	Adult	Terrestrial	22.7	Lepidoptera	Larvae	Terrestrial	13.3	
Diptera	Larvae	Aquatic	13.4	Diptera	Adult	Terrestrial	10.8	
Hymenoptera	Adult	Terrestrial	3.7	Ephemeroptera	Larvae	Aquatic	8.9	
Trichoptera	Larvae	Aquatic	3.3	Trichoptera	Larvae	Aquatic	8.5	
Plecoptera	Larvae	Aquatic	2.8	Diptera	Larvae	Terrestrial	5.5	
Hemiptera		Terrestrial	1.8	Plecoptera	Larvae	Aquatic	2.7	
Malocostraca		Aquatic	1.5	Hymenoptera	Adult	Terrestrial	1.8	
Diptera	Larvae	Terrestrial	1.3	Araneae		Terrestrial	1.0	
Lepidoptera	Larvae	Terrestrial	0.9	Opiliones		Terrestrial	0.8	
Other			2.6	Other			2.7	
Rocky Run, dist	urbed sectio	n, median fis	h	Rocky Run, refe	rence sectio	n, median fis	h	
condition: 0.9	76			condition: 1.0	15			
Diptera	Larvae	Aquatic	36.3	Ephemeroptera	Larvae	Aquatic	27.3	
Diptera	Adult	Terrestrial	25.7	Diptera	Adult	Terrestrial	15.3	
Ephemeroptera	Larvae	Aquatic	8.3	Diptera	Larvae	Aquatic	12.4	
Diptera	Larvae	Terrestrial	7.8	Lepidoptera	Larvae	Terrestrial	11.3	
Lepidoptera	Larvae	Terrestrial	6.9	Diptera	Larvae	Terrestrial	11.0	
Trichoptera	Larvae	Aquatic	4.0	Hemiptera		Terrestrial	10.6	
Hymenoptera	Adult	Terrestrial	3.9	Hymenoptera	Adult	Terrestrial	2.7	
Araneae		Terrestrial	1.7	Trichoptera	Larvae	Aquatic	2.6	
Hymenoptera	Larvae	Terrestrial	1.1	Ephemeroptera	Adult	Terrestrial	1.4	
Hemiptera		Aquatic	0.9	Plecoptera	Larvae	Aquatic	1.3	
Other			3.4	Other			4.1	
Schoolcraft Run,	disturbed sec	tion, median	fish	Schoolcraft Run, reference section, median fish				
condition: 1.03	8			condition: 0.97	3			
Ephemeroptera	Larvae	Aquatic	69.0	Diptera	Adult	Terrestrial	22.8	
Diptera	Adult	Terrestrial	6.7	Diptera	Larvae	Aquatic	16.0	
Trichoptera	Larvae	Aquatic	5.6	Diptera	Larvae	Terrestrial	11.6	
Coleoptera	Adult	Terrestrial	4.0	Hymenoptera	Adult	Terrestrial	11.6	
Hemiptera		Terrestrial	2.8	Ephemeroptera	Larvae	Aquatic	10.1	
Diptera	Larvae	Aquatic	2.6	Lepidoptera	Larvae	Terrestrial	7.3	
Hymenoptera	Adult	Terrestrial	1.9	Trichoptera	Larvae	Aquatic	6.6	
Lepidoptera	Larvae	Terrestrial	1.9	Hymenoptera	Larvae	Terrestrial	2.7	
Diptera	Larvae	Terrestrial	1.4	Plecoptera	Larvae	Aquatic	2.6	
Hemiptera		Aquatic	1.0	Hemiptera		Terrestrial	1.8	
Other			3.1	Other			6.9	

fish growth rates (Xu et al. 2010; Courtwright and May 2013), but of the three streams, Rocky Run (where disturbance decreased fish condition) has the deepest pools and highest flow (Studinski 2010). Water temperature affects the metabolic demand of brook trout, but Rocky Run had the coolest water, while fish condition improved in the disturbed reaches of the warmer Schoolcraft Run (Tables 1 and 3). The treatments were previously found to have no effect on sedimentation (Studinski et al. 2012) and caused similar increases to periphyton biomass (Table 5).

In streams impacted by acid deposition, it may be more difficult for fish to cope with the increased metabolic demands that are commonly associated with riparian disturbance. Rocky Run, where fish condition was negatively affected by riparian disturbance, was the only stream where fish diet composition did not differ between the disturbed and reference reaches. Most ephemeropterans are periphyton grazers, but despite an increase in periphyton that exceeded that in the other two streams, ephemeropterans in Rocky Run did not increase in biomass as much as in Mitchell Lick and Schoolcraft Run (Table 5). Of particular importance within Ephemeroptera may be the very low Baetidae abundance in the disturbed section of Rocky Run (0.2/m²) when compared to Schoolcraft Run (121.3/m²) and Mitchell Lick (26.0/m²) (Studinski 2010). The absence of a baetid response to disturbance in Rocky Run may be due to lower pH, as Baetidae are known to be an acid-sensitive taxa (Tabak and Gibbs 1991, Lepori

and Ormerod 2005). Lacking an increase in the secondary productivity of grazing Ephemeroptera and therefore the associated shift in diet, age-0 brook trout in the disturbed reach of Rocky Run decreased in condition due to the increased metabolic demands of stream warming.

The increased energy content and availability of Ephemeroptera makes them a critical food source for fish coping with increased metabolic demands. Other researchers have also observed increases in Ephemeroptera biomass following riparian logging (Wallace and Gurtz 1986; Stone and Wallace 1998). Similar to the results presented here, Wilson et al. (2014) observed a shift in brook trout diets favoring Ephemeroptera larvae following riparian disturbance. Ephemeroptera typically have a higher energy content than other prey like detritivores (Cummins and Wuycheck 1971), actively enter drift (Kohler 1985), are often multivoltine, and may be more susceptible to predation in highproductivity streams (Kohler and McPeek 1989). Since there was no difference in the mass of stomach contents between the disturbed and reference sections of these streams, the successful strategy for age-0 brook trout appears to be focusing on the newly abundant Ephemeroptera (Table 2) and not simply increasing the overall amount of biomass consumed.

Although increased consumption of Ephemeroptera appeared to allow age-0 brook trout to tolerate, and in some instances benefit from, the canopy reduction and subsequent stream warming



Fig. 2. Mean relative condition of age-0 brook trout with 95% confidence intervals shown. Condition varied significantly, but inconsistently, by stream and month. Condition also varied by treatment (disturbed versus reference) in Rocky Run and Schoolcraft Run. Letters represent the results of post-hoc comparisons, which were adjusted for multiple comparisons.

Table 3. Relative condition, length, and weight of age-0 brook trout averaged across months (June-September) from three central Appalachian streams.

	Treatment	Relative condition mean ± SE	Length (mm) mean ± SE	Weight (g) mean ± SE
Mitchell Lick	Disturbed	0.998±0.096	68.2±8.4	3.2±1.1
	Reference	0.994±0.093	65.8±7.6	2.8±0.9
Rocky Run	Disturbed	0.984±0.100	63.3±7.8	2.5±1.0
	Reference	1.014±0.097	66.8±9.4	3.1±1.3
Schoolcraft Run	Disturbed	1.049±0.098	75.7±9.0	4.5±1.6
	Reference	0.986±0.098	71.0±8.8	3.6±1.5

caused by riparian disturbance, Fig. 3 suggests a nonlinear relationship and an upper limit to the benefits of focusing on Ephemeroptera. As a stream warms and possibly exceeds the upper thermal preference for age-0 brook trout, increased production and consumption of ephemeropteran larvae will eventually not be able to counteract the increased metabolic demands.

Riparian disturbance affected age-0 brook trout diets and condition, and this study observed all possible outcomes (positive effect, negative effect, and no effect) within three superficially similar streams. This suggests that additional mechanisms underlie the response of stream food webs to riparian disturbance, and stream parameters like pH and temperature should be considered

Schoolcraft Run

Table 4. Akaike information criterion (AIC) values along with Δ AIC scores for each individual model tested.

Model	AIC	ΔAIC
Kn = Month × stream + month × treatment +	-1237.1	0
stream × treatment	1000 5	
Kn = Month × stream + stream × treatment	-1232.6	4.5
$Kn = Month \times treatment + stream \times treatment$	-1218.3	18.8
$Kn = Month + stream \times treatment$	-1214.5	22.6
$Kn = Month \times ttream + month \times treatment$	-1211.6	25.5
Kn = Stream × treatment	-1210.0	27.1
Kn = Treatment + month × stream	-1209.2	27.9
$Kn = Month \times stream$	-1207.1	30.0
Kn = Stream + month × treatment	-1194.3	42.8
Kn = Month + treatment + stream	-1192.4	44.7
$Kn = Month \times treatment$	-1191.5	45.6
Kn = Month + stream	-1190.2	46.9
Kn = Month + treatment	-1189.8	47.3
Kn = Stream + treatment	-1188.1	49.0
Kn = Month	-1187.7	49.4
Kn = Stream	-1186.0	51.1
Kn = Treatment	-1185.3	51.8
Kn = 1	-1183.2	53.9

Note: The dependent variable in all models is relative fish condition (Kn) of brook trout from three central Appalachian streams.

	Treatment	Aquatic invertebrates (mg dry weight/m²)	Ephemeroptera (mg dry weight/m²)	Terrestrial invertebrate input (mg dry weight/m² per day)	Periphyton AFDM (mg/m²)	Age-0 brook trout/250 m, mean ± SE
Mitchell Lick	Disturbed	186.9	62.6	22.1	0.20	63±10
	Reference	209.2	24.9	14.1	0.10	51±20
Rocky Run	Disturbed	113.1	27.6	24.0	0.35	33±8
	Reference	61.6	10.8	11.4	0.05	38±18
Schoolcraft Run	Disturbed	235.0	122.6	26.5	0.23	69±21
	Reference	204.2	67.2	8.8	0.12	57±19

Note: Invertebrate data were collected 2 years prior to the collection of brook trout diets. Aquatic invertebrate data are summarized from Studinski (2010), while terrestrial invertebrate data are from Studinski and Hartman (2014). Periphyton data as ash-free dry mass (AFDM) are from Studinski (2010).

Fig. 3. Median age-0 brook trout condition for each reach in each stream and month plotted against the relative importance of larval Ephemeroptera in the diets of those fish (top graph). Also included is observed median relative condition plotted against predicted median relative condition resulting from the nonlinear regression analysis represented in the top graph (bottom graph).



when attempting to predict or minimize the effects of riparian disturbance. In streams with favorable water quality characteristics, age-0 brook trout may benefit from intense but spatially limited disturbance, while fish in more acidic streams, or streams with summer temperatures already near age-0 brook trout thermal limits, could be harmed. Predicting the effects of disturbance on stream food webs is a difficult proposition. A more expansive study across a range of stream temperatures and pH values would be a time-consuming but valuable addition to this field of research.

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