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Fish introductions and light modulate food web fluxes in tropical streams: a whole-ecosystem experimental approach

Sarah M. Collins,[1,2,12] Steven A. Thomas,[3] Thomas Heatherly II,[3,4] Keeley L. MacNeill,[1] Antoine O. H. C. Leduc,[1,5] Andrés López-Sepulcre,[6,7] Bradley A. Lamphere,[8] Rana W. El-Sabaawi,[9] David N. Reznick,[10] Catherine M. Pringle,[11] and Alexander S. Flecker[1]

[1]*Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA*
[2]*Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources, East Lansing, Michigan 48824 USA*
[3]*School of Natural Resources, University of Nebraska-Lincoln, Hardin Hall Room 403, Lincoln, Nebraska 68583 USA*
[4]*Department of Ecology, State University of Rio de Janeiro, 524 Rua São Francisco Xavier, Rio de Janeiro, Rio de Janeiro 20550-013 Brazil*
[5]*Institute of Biology, Federal University of Bahia, Ondina Campus, Rua Barão de Geremoabo, 147, Salvador, Bahia 40170-290 Brazil*
[6]*CNRS UMR 7618, Institute of Ecology and Environmental Sciences Paris (iEES), Université Pierre et Marie Curie, 7 Quai Saint Bernard, Paris 75252 France*
[7]*Deptartment of Biological and Environmental Sciences, University of Jyväskylä, PO Box 35, Jyväskylä 40014 Finland*
[8]*Biology Department, College of William and Mary, Williamsburg, Virginia 23187 USA*
[9]*Department of Biology, University of Victoria, PO Box 1700 STN CSC, Victoria, British Columbia V8W 2Y2 Canada*
[10]*Department of Biology, University of California Riverside, 209 University Laboratory Building, Riverside, California 92521 USA*
[11]*Odum School of Ecology, University of Georgia, Athens, Georgia 30602 USA*

Abstract. Decades of ecological study have demonstrated the importance of top-down and bottom-up controls on food webs, yet few studies within this context have quantified the magnitude of energy and material fluxes at the whole-ecosystem scale. We examined top-down and bottom-up effects on food web fluxes using a field experiment that manipulated the presence of a consumer, the Trinidadian guppy *Poecilia reticulata*, and the production of basal resources by thinning the riparian forest canopy to increase incident light. To gauge the effects of these reach-scale manipulations on food web fluxes, we used a nitrogen (^{15}N) stable isotope tracer to compare basal resource treatments (thinned canopy vs. control) and consumer treatments (guppy introduction vs. control). The thinned canopy stream had higher primary production than the natural canopy control, leading to increased N fluxes to invertebrates that feed on benthic biofilms (grazers), fine benthic organic matter (collector-gatherers), and organic particles suspended in the water column (filter feeders). Stream reaches with guppies also had higher primary productivity and higher N fluxes to grazers and filter feeders. In contrast, N fluxes to collector-gatherers were reduced in guppy introduction reaches relative to upstream controls. N fluxes to leaf-shredding invertebrates, predatory invertebrates, and the other fish species present (Hart's killifish, *Anablepsoides hartii*) did not differ across light or guppy treatments, suggesting that effects on detritus-based linkages and upper trophic levels were not as strong. Effect sizes of guppy and canopy treatments on N flux rates were similar for most taxa, though guppy effects were the strongest for filter feeding invertebrates while canopy effects were the strongest for collector-gatherer invertebrates. Combined, these results extend previous knowledge about top-down and bottom-up controls on ecosystems by providing experimental, reach-scale evidence that both pathways can act simultaneously and have equally strong influence on nutrient fluxes from inorganic pools through primary consumers.

Key words: *nitrogen flux; reach-scale experiment; stable isotope tracers; stream food web; top-down and bottom-up effects; trophic linkages; benthic macroinvertebrates, primary production, Trinidad guppy, Neotropics, 15N.*

Introduction

The relative importance of top-down and bottom-up effects have been studied, debated, and reviewed extensively in the ecological literature (e.g., reviews by Power 1992, Hairston and Hairston 1993, Polis and Strong 1996, Gruner et al. 2008). There is substantial evidence that both pathways are important in structuring ecosystems (Leroux and Loreau 2015). Many seminal studies have been conducted in freshwater systems (reviewed by Taylor et al. 2015), where investigators have documented significant effects of predatory or planktivorous fishes (Carpenter and Kitchell 1988, Power 1990, Flecker and Townsend 1994), nutrient enrichment (Schindler 1977, Hambright et al. 2007, Davis et al. 2010), and light availability (Hill et al. 1995, Ask et al. 2009, De

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[12]Present address: University of Wisconsin Center for Limnology, 680 North Park Street, Madison, Wisconsin 53706 USA. E-mail: sarahmcollins@gmail.com

Nadai-Monoury et al. 2014). Many of these studies also demonstrate significant effects on functional properties such as consumer growth, primary production and decomposition, yet relatively little is known about how top-down and bottom-up drivers influence fluxes of energy and materials in food webs, especially at the natural ecosystem scale.

Even though the relative effects of top-down and bottom-up drivers on ecosystem fluxes are poorly described, there is considerable evidence that energy and material fluxes through food webs vary with environmental conditions (e.g., Cebrian 1999, Davis et al. 2010, Cross et al. 2013, Taylor et al. 2015). Differences in flux rates can be associated with changes in consumer assemblages that alter the strength of top-down forces; for example, altered species assemblages due to environmental contaminants (Sherwood et al. 2002), hydrologic alteration of rivers (Cross et al. 2013), and disease-driven species losses (Whiles et al. 2013) can all lead to differences in the energy or material linkages in food webs. Bottom-up effects, such as increased nutrient concentrations, also alter the magnitude (Cross et al. 2006, Davis et al. 2010) and stability (Rosenzweig 1971) of food web linkages. Quantifying ecosystem flux rates in natural ecosystems can be methodologically challenging, but isotope tracer approaches offer a quantitative method for characterizing food web linkages (e.g., Nadelhoffer et al. 1999, Veuger et al. 2007, Dodds et al. 2014). Unlike studies of natural isotope abundance, tracer additions can be used to estimate nutrient fluxes between food web compartments. Isotope tracer additions offer a promising approach to elucidate how environmental changes alter ecosystem fluxes. Tracer techniques have been used in many stream ecosystem studies, but rarely in combination with an ecosystem-scale experimental manipulation.

Here, we evaluate the interactive effect of increased light availability and an introduced consumer, the guppy *Poecilia reticulata*, on N fluxes in stream food webs using a whole-ecosystem experiment combined with ^{15}N isotope tracer additions. Assays assessing nutrient limitation suggest that streams in our study area are more limited by light than nutrients (T. Heatherly, *unpublished data*) so increased light availability is likely to be an important bottom-up force and lead to increased primary production. Guppies are well suited for field introduction experiments and Trinidad's unique geomorphology contains frequent barrier waterfalls that allow guppies to be confined to a study reach (Reznick et al. 1996). Guppy evolution, life history, morphology, and diet have been well characterized in previous field experiments (e.g., Reznick et al. 1990, reviewed by Magurran 2005). Research in artificial streams suggests that guppies strongly influence ecosystem processes, leading to significant effects on the biomasses of algae and other consumer species (Palkovacs et al. 2009, Bassar et al. 2010, El-Sabaawi et al. 2015). The effect of guppies on natural stream ecosystems is not as well understood, but field observations (Walsh et al. 2011, Zandona et al. 2011, Kohler et al. 2012) and small-scale consumer-exclusion experiments (Marshall et al. 2012) show that guppies can have a strong effect on stream ecosystems, including effects on biofilm accrual, leaf decomposition, and the abundance of other fish species. Light conditions and fish assemblages often covary in Trinidadian streams, so top-down and bottom-up effects cannot be disentangled with survey studies alone (Grether et al. 2001), but no previous work has used stream-reach-scale experiments to compare the effects of guppies and light.

We present results from nitrogen (^{15}N) isotope additions performed in four stream reaches that were part of a whole-ecosystem experiment that we conducted in two headwater streams. Specifically, we thinned the riparian canopy of one stream to increase light availability, and introduced guppies to the lower section of both streams, which were separated from an upstream guppy-free section by barrier waterfalls. We predicted that increased light availability would boost primary production and subsequently increase fluxes of energy and materials from algal dominated biofilms to grazing primary consumers. Previous experiments in artificial streams demonstrate that guppy presence reduced biofilm chlorophyll standing stocks and areal primary production rates, but increased primary production efficiency (i.e., chlorophyll-specific primary production rate; Bassar et al. 2010). Thus we predicted that guppy introduction would also affect reach-scale primary production and nitrogen fluxes from biofilms to invertebrate primary consumers. Our overarching objective was to expand our current understanding of top-down and bottom-up forces by combining ecosystem-scale manipulations and isotope tracer techniques that provide estimates of food web flux rates at the reach scale.

Methods

Study site and ecosystem manipulation

We conducted this study in ~200 m reaches of two streams in an undeveloped area of the Guanapo Valley in the Northern Range of Trinidad during the 2010 dry season (March–May). The two streams are parallel, headwater tributaries of the Guanapo River located less than 1 km apart (study site map in Appendix S1), and have low to moderate nutrient concentrations (Table 1). Prior to manipulation, both streams were heavily shaded by riparian canopy, and killifish (*Anablepsoides hartii*) were the only resident fish species. Other fish species were prevented from upstream movement into the study reaches by downstream waterfalls that are barriers to upstream migration.

Using a 2 × 2 factorial design, we selectively manipulated ambient light availability and the presence of guppies. In 2007, we increased light availability of one of the streams (Upper LaLaja, hereafter thinned canopy stream) by thinning the canopy along a reach of stream approximately 200 m long, i.e., removing nearly all trees with a diameter <30 cm within a 5 m distance from the

TABLE 1. Characteristics of four study reaches, including size, stream water chemistry, dry mass of primary uptake components, and stoichiometry of primary uptake components.

Characteristics	Thinned canopy		Natural canopy		Light effect	Guppy effect	Light × guppy interaction
	Guppy introduction	No guppy reference	Guppy introduction	No guppy reference			
Discharge (L/s)	17.6	17.6	13.8	13.8	—	—	—
Stream wetted width (m)	2.58 (1.0)	2.29 (0.78)	1.93 (0.88)	1.89 (0.87)	—	—	—
Depth (cm)	20	20	18	18	—	—	—
Light (moles quanta·m^{-2}·d^{-1})†	12.6 (1.83)	15.5 (5.3)	5.83 (3.61)	7.91 (4.69)	—	—	—
Whole-stream metabolism							
GPP (g O_2·m^{-2}·d^{-1})	3.90 (0.18)	2.45 (0.48)	2.13 (0.62)	1.60 (0.26)	$F_3 = 86.9$, $P < 0.01$, all pairwise comparisons $P < 0.01$	$F_3 = 86.9$, $P < 0.01$, all pairwise comparisons $P < 0.01$	$F_3 = 86.9$, $P < 0.01$, all pairwise comparisons $P < 0.01$
R (g O_2·m^{-2}·d^{-1})	26.2 (0.73)	15.9 (0.78)	24.3 (1.8)	28.1 (1.2)	$F_3 = 101.2$, $P < 0.01$, all pairwise comparison $P < 0.05$	$F_3 = 101.2$, $P < 0.01$, all pairwise comparison $P < 0.05$	$F_3 = 101.2$, $P < 0.01$, all pairwise comparison $P < 0.05$
Biomass-specific GPP (g O_2·m^{-2}·d^{-1}·g^{-1}·m^{-2})	0.125	0.050	0.069	0.034	—	—	—
Stream chemistry							
NH_4 (μg/L)	2.58	2.16	3.45	2.68	—	—	—
NO_3 (μg/L)	213	218	200	204	—	—	—
SRP (μg/L)	23.8	23.6	37.3	29.1	—	—	—
DOC (mg/L)	0.582 (0.027)	0.582 (0.027)	0.626 (0.073)	0.626 (0.073)	—	—	—
Primary uptake, dry mass							
Epilithon AFDM (g/m^2)	31.1 (40)	48.9 (46)	30.7 (22)	46.5 (38)	NS	NS	NS
Epilithon chl *a* (mg/m^2)	14.6 (19)	14.1 (12)	11.6 (7.2)	13.3 (13)	NS	NS	NS
CBOM (g/m^2)	70.9 (67)	86.3 (121)	131 (114)	71.5 (57)	NS	NS	NS
FBOM (g/m^2)	701 (492)	2,026 (1,418)	—	—			
Seston (mg/L)	0.893 (0.34)	0.505 (0.22)	0.388 (0.19)	1.49 (0.54)	$F_3 = 5.92$, $P = 0.02$	$F_3 = 5.92$, $P = 0.02$	NS

Notes: Means are for a pooled sample of three replicates per reach on each of two sampling dates (March, May) with standard deviations in parentheses. Significant contrasts identified from linear models described in the results section are noted in the right column. Nonsignificant contrasts are denoted by "NS". GPP, gross primary productivity; ER, ecosystem respiration; SRP, soluble reactive phosphorus; DOC, dissolved organic carbon; AFDM, ash-free dry mass; CBOM, coarse benthic organic matter; FBOM, fine benthic organic matter.

† Photosynthetically active radiation (PAR).

stream. We maintained the open canopy through continued removal of vegetation from 2007 to 2010. In contrast, no canopy manipulations were conducted on the second stream, Lower LaLaja (hereafter, natural canopy stream), although some light gaps formed by natural tree falls. We continuously monitored light using Hobo light loggers and monitored discharge using Hobo stage loggers (Onset Computer Corporation, Bourne, Massachusetts, USA). We converted data from Hobo light loggers (lumen units) to photosynthetically active radiation (PAR) using methods described by Thimijan and Heins (1983). Experimental thinning increased the flux of PAR by 30% in the thinned canopy stream and the treatment remained consistent from 2007 to 2010 (Kohler et al. 2012). Incident PAR in the thinned canopy stream was approximately two times higher than PAR in the natural canopy stream during this experiment in the 2010 dry season (Table 1).

During the isotope tracer releases in March 2010, we quantified primary production in each study reach through whole-stream metabolism measurements. Gross primary production (GPP) and ecosystem respiration (ER) rates were determined using an open-system, single-station, diel approach (Odum 1956, Roberts et al. 2007). GPP and ER rates were determined using the modeling approach described by Hotchkiss and Hall (2015). We confirmed that a single station metabolism approach was appropriate for our study design by using methods described by Holtgrieve et al. (2010) to estimate the reach length influencing dissolved oxygen concentrations. Methods for metabolism measurements are described in detail in Appendix S2.

Both streams were divided into a guppy introduction reach ("introduction reach") and an upstream control reach ("no guppy control") separated by barriers that impeded upstream migration of guppies. Guppies were

introduced to the lower reach of both study streams in March 2008. Following their introduction, guppy populations were monitored monthly through mark–recapture techniques, and increased in density annually through 2010 (Travis et al. 2014). Guppies were not observed in the control reaches before or during the study period. The combination of canopy and guppy treatments resulted in four distinct study reaches: canopy thinned stream, guppy introduction reach (thinned, guppy), canopy thinned no guppy control reach (thinned, no guppy), natural canopy guppy introduction reach (canopy, guppy), and natural canopy no guppy control reach (canopy, no guppy). Each study reach was approximately 60–80 m long.

Food web biomass and water chemistry sampling

Biomass of food web compartments and water chemistry in all study reaches were monitored immediately before and after the isotope tracer study period. Each stream had six biomass sampling sites, three in the guppy introduction reach and three in the upstream control reach. Sampling sites were located equidistant (approximately 20–30 m apart) along each study reach. We sampled one pool and one riffle habitat at each of the six sampling sites for a total of 12 samples per stream. Each biomass sample included basal resources (epilithon, fine benthic organic matter, leaf litter, water column organic matter) and invertebrates. Biomass sampling methods for basal resources and invertebrates are described in detail in Appendix S3. Biomass estimates for fish (guppies and killifish) were obtained from concurrent mark–recapture studies in both streams (methods detailed in Fraser and Lamphere 2013, López-Sepulcre et al. 2013, Travis et al. 2014).

Additionally, we collected filtered water samples for ammonium (NH_4), soluble reactive phosphorus (SRP), and nitrate (NO_3) analyses. Ammonium was analyzed in the field using fluorometric methods with an Aquaflor handheld fluorometer (Turner Designs, Sunnyvale, California, USA). Nitrate and SRP samples were frozen for subsequent laboratory analysis. We analyzed nitrate using a Dionex ICS-90 ion chromatography system with Chromeleon software (Dionex Corporation, Sunnyvale, California, USA), and SRP on a Pharmacia LKB Ultraspec III spectrophotometer (model 80-2097-62; Pharmacia Biotech, Piscataway, New Jersey, USA) using a molybdenum blue method developed by Murphy and Riley (1962).

^{15}N-ammonium addition to quantify food web fluxes

We added ^{15}N labeled ammonium (as dissolved $^{15}NH_4Cl$, 98 atom %; Sigma Aldrich, St Louis, Missouri, USA) to all four study reaches. Over a 10-day period (7–16 March 2010), we added isotope tracer using a continuous drip at a rate of 10 mL/min. The tracer addition increased the $\delta^{15}N$ of dissolved ammonium to approximately 20,000‰. The target enrichment was not intended to fertilize the system, and the concentration of ^{15}N added represented an increase in ambient NH_4^+-N concentration of ~8% (Table 1). Throughout the course of the isotope release, we evaluated dilution effects along the study reaches by adding rhodamine (a fluorescent dye) as a conservative tracer.

To track the fate of the isotope tracer, we sampled food web compartments at three stations located approximately 15, 30, and 60 m downstream from the point of isotope release in each sample reach. Samples were collected on three days during the 10-day isotope release (Days 3, 7, and 10) and on five days during the month following the isotope release (Days 13, 17, 20, 30, and 40). Sampled food web compartments included: dissolved inorganic nitrogen ($^{15}NO_3^-$ and $^{15}NH_4^+$), epilithon, fine benthic organic matter (FBOM; sampled from the sediment surface via suction), leaf litter, seston, eight common invertebrate taxa representing five functional feeding groups, guppies, and killifish. Invertebrate taxa selected were sufficiently large bodied and abundant that they could be collected by hand with minimal disturbance to the streambed. While we selected most invertebrate taxa because they were biomass dominant (*Eudaniela*, *Euthyplocia*, *Psephenus*, *Leptonema*, *Tricorythodes*, and *Argia*, biomass data in Appendix S3), we selected two additional invertebrate taxa, *Petrophila* sp. and *Phylloicus* sp. because they represented distinct functional feeding groups (scraper and shredder, respectively). We were unable to collect and analyze some small-bodied but abundant taxa (e.g., chironomids) because collecting enough individuals for isotope sample analysis would have resulted in major disturbance to the streambed.

We sampled guppies and killifish on a subset of collection days (Days 10, 20, 30, 40 for killifish and Days 10, 25, and 40 for guppies). We also collected background samples from each food web compartment to correct for background isotopic values. Background samples were collected either prior to the start of the experiment or from upstream of the tracer addition point in the no-guppy control reaches.

We dried all samples at 50°C and conducted isotopic analyses at the University of Georgia Analytical Chemistry Laboratory. We also used elemental analysis data from isotope analyses to quantify the ratio of carbon to nitrogen (C:N) in basal resources, which is often used as a proxy of food quality. Basal resource sampling protocols were the same as the biomass sampling techniques, but for invertebrates, we hand-picked individuals from rocks to ensure that sufficient numbers of each taxon were collected for isotopic analysis. We also measured water column $\delta^{15}N$, which we measured with a filter pack diffusion technique (Sigman et al. 1997, Holmes et al. 1998). Specifically, we collected 900 mL of water in 1-L plastic cubitainers for $\delta\ ^{15}NH_4$ samples and added a 60-μg spike of N, as NH_4, to increase N mass to a level that is detectable by a mass spectrometer. We collected 500 mL of water for $\delta^{15}NO_3$ samples and transferred samples in 250-mL high density polyethylene bottles after boiling to reduce volume to approximately 100 mL.

Ammonium from all samples was allowed to diffuse onto a 1.0-cm Whatman GF/D (2.7-μm pore size) filter sealed in polytetraflourethylene tape for at least 3 weeks before filters were harvested and dried at 50°C.

Turnover and flux calculations

Turnover rates (k) for primary uptake compartments were calculated using an exponential decline model fit to data from the days that followed the isotope tracer release (i.e., drip days 11–40). Turnover was estimated as the negative slope of a linear regression of log-transformed $\delta^{15}N$ data over time. Exponential decline models are effective for primary uptake compartments with rapid turnover rates, but not for consumers that retain isotope label at the end of the experiment (Whiles et al. 2013).

We used a dynamic compartment model to calculate turnover and flux rates of consumers, as described in detail by Dodds et al. (2014). Briefly, we used observed patterns of ^{15}N accumulation and loss in a given taxon and its presumed food source over the course of our tracer release and post-release sampling period. We estimated uptake and loss rates by converting calculating $\delta^{15}N$ to atomic ratios, then calculating a flux rate of ^{15}N and ^{14}N from the food pool into the consumer pool between each sampling date. The equation describing the change in ^{15}N of the consumer pool is as follows:

$$\mathrm{CP}_{15\mathrm{N},t=2} = \mathrm{CP}_{15\mathrm{N},t=1} + (U \times \mathrm{ARFP} \times t) - (L \times \mathrm{ARCP} \times t)$$

where CP is the size of the consumer pool at different time steps, U is the uptake rate, ARFP is the atomic ratio of the food pool, L is the loss from the consumer pool, and ARCP is the atomic ratio of the consumer pool. We accounted for the change in ^{15}N in the consumer after each time step to calculate the new beginning size of the consumer pool for the following time step. Similarly, we described the change in ^{14}N of the consumer pool as follows:

$$\mathrm{CP}_{14\mathrm{N},t=2} = \mathrm{CP}_{14\mathrm{N},t=1} + (U \times [1 - \mathrm{ARFP}] \times t) - (L \times [1 - \mathrm{ARCP} \times t)$$

The number of time steps for each model usually included five to eight samples at a frequency of 3–10 d between samples, depending on sample availability. We used the Solver function in Microsoft Excel (Microsoft, Redmond, Washington, USA) to change U to minimize the sum of error terms for each time step, and visually checked that observed and modeled patterns of $\delta^{15}N$ were similar. Fitting a model using Solver has proven effective for other isotope tracer data sets with sampling frequencies similar to ours, including data from 19 streams in temperate and tropical regions across the world (Dodds et al. 2014). We calculated a taxon-specific turnover rate (percentage of N per day) for each consumer at each downstream sampling station, and calculated the average turnover rate for that taxon for each reach. To calculate a taxon-specific flux rate (mg $N \cdot m^{-2} \cdot h^{-1}$), we multiplied the average taxon-specific turnover rate for the reach by the average N mass for that taxon.

We estimated diet information for the model based on feeding mode of invertebrates, qualitative inspection of gut contents, and literature values of diet proportions (e.g., Zandona et al. 2011). For omnivores that consume multiple food sources, we weighed each individual food source based on estimated diet proportions in the diet to create a composite food pool for the consumer. All diet proportions and food web model inputs are described in detail in Appendix S4.

We compared primary production, biomasses, turnover, and flux rates among treatment reaches using fixed-effects linear models using the lm function in R, with the three sampling transects per study reach as the unit of replication. Light and guppy treatments were included as fixed factors, and their interaction was only included when significant. It should be noted that this design treats each transect as an independent replicate, yet transects in the same stream reach are not entirely independent. It was not possible to conduct more simultaneous ^{15}N experiments, so each treatment combination is only represented by a single stream reach, leaving within-stream transects as our only possible unit of replication. The unit of replication for ecosystem metabolism data was sampling day rather than sampling station, with metabolism measurements made in all reaches on five common days over the course of the study. Hence, we evaluated metabolism data using a repeated-measures ANOVA design, using the aov function in R, and used post hoc pairwise t tests to compare treatment reaches. We corrected all P values for multiple comparisons using Benjamini and Hochberg's false discovery rate method (Benjamini and Hochberg 1995). We calculated effect size (Cohen's d) to compare the relative strength of differences between guppy and light reaches on N fluxes to consumers. All statistical tests were conducted in R version 3.1.2 (R Core Team 2014).

Results

Primary production was higher in the thinned canopy stream compared to the natural canopy stream, and higher in guppy introduction reaches compared to no-guppy control reaches. Higher daytime photosynthetically active radiation (PAR) in the thinned canopy stream compared to natural canopy stream (Table 1) corresponded with significantly higher gross primary production (GPP) and lower rates of ecosystem respiration (ER) during the 2010 March–May dry season period. Differences in GPP among reaches, however, did not result in significantly different amounts of epilithon chlorophyll a or AFDM (statistical comparisons in Table 1). Introduced guppy populations in our two study streams reached a peak during the 2010 dry season compared with other population estimates between 2008 and 2011 (Travis et al. 2014), with guppy biomass estimates of 2.86 and 1.43 g/m^2 in the thinned canopy

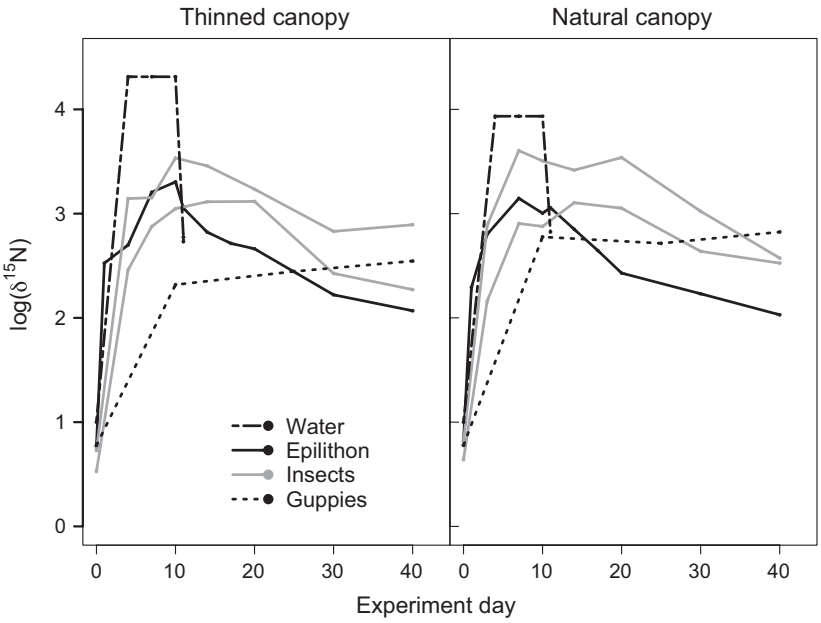

FIG. 1. We detected isotope tracer ($\delta^{15}N$) in all food web compartments. Isotope enrichment over time for subset of food web compartments (water, epilithon, two primary consumer insects, guppies) is shown for canopy thinned and natural canopy streams. Both insect species are shown in gray; *Tricorythodes* is the more enriched line and *Petrophila* is the less enriched line in both panels.

stream and the natural canopy stream, respectively. GPP and ER were also significantly higher in guppy introduction reaches compared to upstream control reaches without guppies (statistical comparisons in Table 1), but guppy introduction and guppy-free control reaches did not differ in the standing stock of chlorophyll *a* or epilithon AFDM (Table 1). Biomass of coarse benthic organic matter (CBOM) did not differ among any of the study reaches. Seston biomass differed among all reaches, with dry mass declining in the following order: canopy, no guppy > thinned, guppy > thinned, no guppy > canopy, guppy (Table 1).

The isotope tracer release resulted in substantial enrichment of all sampled food web compartments in the four study reaches in $\delta^{15}N$ (Fig. 1). In many cases, invertebrate primary consumers were more enriched in ^{15}N than presumed bulk food sources, but much less enriched than water column ^{15}N-NH_4 (Fig. 1). Compared to background levels (represented by data on Day 0, which were collected before the tracer release began), guppies and killifish also became enriched at levels of several hundred per milliliter (Fig. 1).

Turnover times of basal resource compartments varied for each compartment, with fastest turnover of CBOM, moderate turnover of epilithon and seston and slow turnover of FBOM (fixed effects linear model, $F = 7.4$, df = 3, $P < 0.001$, Table 2). Areal uptake rates of N into basal resource compartments also varied by compartment, with high uptake rates to FBOM and CBOM due to their relatively high biomass, moderately low uptake rates for epilithon, and very low uptake rates for seston (fixed effects linear model, $F = 13.8$, df = 3, $P < 0.001$, Table 2).

Our invertebrate sampling included many of the biomass-dominant taxa found in both streams (biomass data summarized in Appendix S3). Fluxes are a product of turnover rates and biomass, and both turnover and biomass varied among study reaches depending on the taxon (Table 2). Fluxes of N from primary uptake compartments to primary consumers differed by invertebrate taxon, stream, and guppy vs. control reach (Fig. 2, statistical contrasts detailed for each species in Table 3). Grazers, collector-gatherers, and collector-filterers had significantly higher N fluxes in the thinned canopy stream than the natural canopy stream, and significantly higher N fluxes in guppy reaches than in control reaches (Table 3). We detected no differences in N flux rates for shredder invertebrates between light or guppy treatment reaches (Fig. 2, Table 3). Fluxes of N to predatory invertebrates (*Argia* damselflies and *Euthyplocia* mayflies) were small relative to primary consumer taxa, guppies and killifish (Appendix S5) and did not differ among reaches with different light or guppy treatments (Table 3). Lastly, N fluxes to killifish did not significantly differ among reaches (Appendix S5, Table 3).

Combined, total reach N fluxes to all consumers were higher in the thinned canopy stream than the natural canopy stream, and higher in guppy introduction reaches than upstream control reaches (Fig. 3). Combined fluxes were particularly high for the thinned-canopy-guppy reach, suggesting a possible interaction between the two treatments (Fig. 3). Across reaches, we observed high areal flux rates of N for guppies, crabs (*Eudaniela*), and mayflies (*Tricorythodes*) relative to other consumer taxa (Fig. 3). Total N flux was much greater in the guppy reach of the thinned canopy stream compared to the reference

TABLE 2. Uptake rates and turnover times of primary uptake compartments and primary consumers in each study reach.

	Thinned canopy		Natural canopy	
Compartment or consumer	Guppy introduction	No guppy reference	Guppy introduction	No guppy reference
Primary uptake				
N uptake rate (mg $N \cdot m^{-2} \cdot d^{-1}$)				
Epilithon	17.6 (12)	24.9 (9.7)	11.6 (3.9)	6.52 (1.3)
CBOM	426 (–)	270 (175)	165 (82)	50.5 (2.4)
FBOM	45.9 (28)	244 (6.2)	78.9 (51)	128 (52)
Seston	0.446 (0.064)	0.222 (0.036)	0.176 (0.031)	0.553 (0.11)
N turnover time (d)				
Epilithon	12.35 (6.9)	15.38 (5.9)	17.24 (7.6)	35.71 (7.0)
CBOM	2.39 (–)	4.29 (3.9)	10.00 (8.8)	17.86 (7.9)
FBOM	71.43 (74.9)	35.71 (10.3)	43.48 (31.6)	29.41 (8.1)
Seston	18.52 (3.2)	16.13 (2.7)	23.26 (8.3)	21.28 (3.7)
Primary consumers				
N uptake rate (mg $N \cdot m^{-2} \cdot d^{-1}$)				
Petrophila	0.566 (0.13)	0.111 (0.03)	0.014 (0.00)	0.012 (0.00)
Psephenus	1.46 (0.51)	0.459 (0.15)	0.478 (0.18)	0.263 (0.09)
Tricorythodes	1.41 (–)	2.83 (0.78)	0.294 (0.01)	0.392 (–)
Leptonema	0.898 (0.07)	0.296 (0.08)	0.810 (–)	0.010 (0.01)
Eudaniela	7.27 (9.7)	2.70 (1.2)	4.10 (–)	4.30 (3.2)
Phylloicus	0.09 (0.02)	0.108 (0.09)	0.114 (0.07)	0.110 (0.01)
N turnover time (d)				
Petrophila	2.26 (0.52)	11.6 (3.0)	7.3 (0.11)	12.6 (8.5)
Psephenus	9.02 (3.1)	30.0 (10.0)	20.2 (9.1)	19.7 (7.3)
Tricorythodes	2.82 (–)	3.68 (0.89)	3.13 (0.16)	6.26 (–)
Leptonema	18.4 (1.4)	10.9 (3.8)	16.3 (10.5)	23.7 (–)
Eudaniela	238 (233)	149 (69)	67 (–)	173 (189)
Phylloicus	12.8 (4.1)	27.3 (23.3)	11.5 (6.9)	7.8 (1.4)

Note: Means are shown with standard deviations in parenthesis.

reach, despite smaller fluxes to *Tricorythodes* mayflies in the guppy introduction reach (Fig. 3). The effect size (Cohen's *d*) of guppy vs. canopy treatments on N flux to consumers differed among consumer taxa (Fig. 4). The largest effect was the guppy effect on N fluxes to filter feeding caddisflies (*Leptonema*), followed by the effect of light on fluxes to collector-gatherer mayflies (*Tricorythodes*). Effects of canopy and guppies were similar for N fluxes to grazer invertebrates (*Psephenus* and *Petrophila*), and effects on fluxes to predators and shredders were small compared to other functional groups (Fig. 4).

Discussion

Our results are consistent with strong and simultaneous bottom-up and top-down effects on nitrogen fluxes through autotrophic food web pathways. In contrast, we found relatively little evidence that light or guppies influenced N fluxes via detrital pathways. The unique combination of stream-reach-scale manipulations of fish and light availability with detailed flux measurements from isotope tracer additions expands our previous knowledge of how consumers and resources influence ecosystems. While the results from this whole-ecosystem experiment are useful for evaluating whether light and guppy effects might occur in natural streams, the lack of replication due to logistical constraints limits us to comparisons of a single reach for each treatment. Despite this trade-off between the benefits of whole-ecosystem manipulations and replication, our evaluation of the magnitude of light and guppy effects on stream ecosystems is consistent with expectations based on theory and concurrent mesocosm experiments (Bassar et al. 2010, Travis et al. 2014, El-Sabaawi et al. 2015), suggesting that results from controlled, replicated experiments scale to natural stream environments.

Increased light availability via canopy thinning was associated with increased N fluxes to some invertebrate taxa relative to natural shaded conditions. Specifically, N flux to larval beetle and moth grazers (*Psephenus* and *Petrophila*) and mayfly collector-gatherers (*Tricorythodes*) was significantly higher in the thinned-canopy stream relative to the natural-canopy stream. Greater N fluxes to grazers in the thinned canopy stream are consistent with light limitation. Interestingly, increased light was also associated with increased N fluxes to collector-gatherers, suggesting that either fine benthic organic matter (FBOM) has an active algal component, or that epilithon and FBOM are closely coupled through growth and

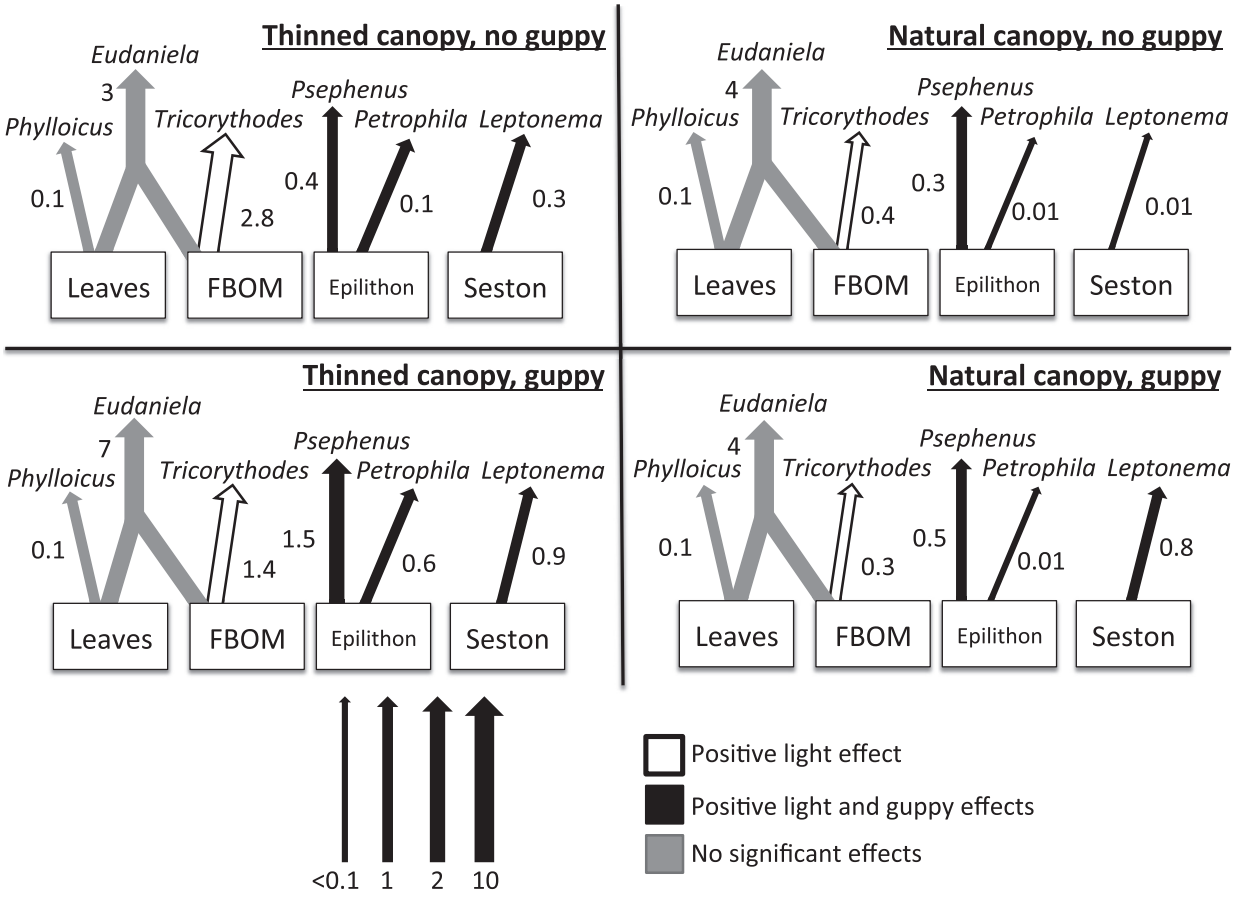

FIG. 2. Flux rates of N to primary consumers in the four study reaches. Numbers next to the lines represent N flux in units of mg $N \cdot m^{-2} \cdot d^{-1}$ and correspond to weight of the line. Colors correspond to significant effects of guppies or light, positive light effects are shown in white, positive light and guppy effects in black, and no effects in gray. FBOM, fine benthic organic matter.

detachment, or both. The significantly higher enrichment of the seston pool and greater N fluxes to caddisfly filter feeders (*Leptonema*) in both reaches of the thinned canopy stream supports the conclusion that epilithon, FBOM, and seston are dynamically linked resources (sensu Cushing et al. 1993, Newbold et al. 2005). Despite increased light availability and elevated primary production, we did not observe a significant increase in the standing stock of epilithon chlorophyll *a* or ash-free dry mass in the thinned canopy stream, indicating a greater N transfer efficiency between epilithon and grazers sampled (Hill et al. 2001, 2010, Kiffney et al. 2004), or that bulk epilithon is too coarse a category to detect the effects of light or fish.

TABLE 3. Results of fixed-effects linear models comparing N fluxes to different invertebrate groups in study reaches.

Taxon	Functional group	Guppy effect	Light effect	Light × guppy interaction
Argia	predator	NS	NS	NS
Eudaniela	detritivore	NS	NS	NS
Euthyplocia	predator	NS	NS	NS
Leptonema	collector-filterer	$F_3 = 169$, $P = 0.005$	$F_3 = 25.3$, $P = 0.03$	NS
Petrophila	grazer	$F_3 = 26.3$, $P = 0.03$	$F_3 = 46.6$, $P = 0.02$	$F_3 = 19.4$, $P = 0.03$
Phylloicus	shredder	NS	NS	NS
Psephenus	grazer	$F_3 = 11.6$, $P = 0.04$	$F_3 = 13.8$, $P = 0.04$	NS
Rivulus	predator	NS	NS	NS
Tricorythodes	collector-gatherer	NS	$F_3 = 19.2$, $P = 0.05$	NS

Notes: Significant contrasts (at the $P < 0.05$ level after correction for multiple comparisons using Benjamini and Hochberg's false discovery rate method) are described. Nonsignificant contrasts are denoted by "NS".

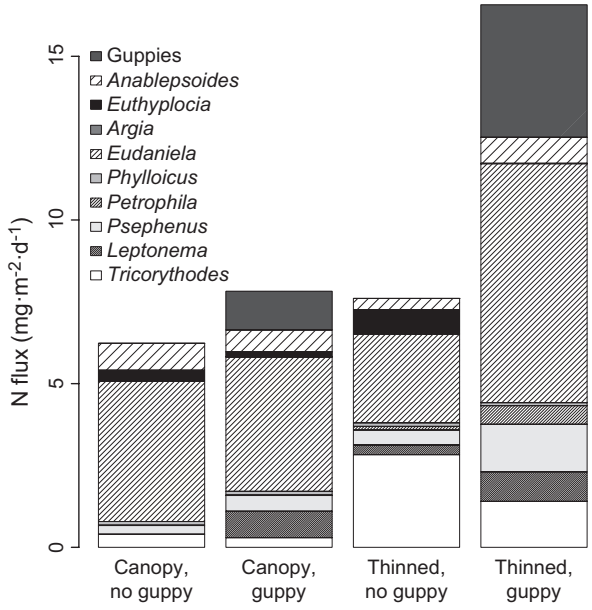

FIG. 3. Combined average N fluxes in different treatment reaches.

We also noted differences in fluxes to several consumer taxa in the guppy introduction reaches relative to the no-guppy control reaches. Specifically, N fluxes to caddisfly filter feeders (*Leptonema* sp.) were higher in the guppy-introduction reaches of both streams compared with control reaches, and the effect size of guppy treatments on N flux to *Leptonema* was higher than any effect on fluxes to any other consumer. Guppies are epibenthic feeders that consume high proportions of fine detritus, so guppy feeding on the benthos likely led to suspension of fine organic matter in the water column. In contrast, N fluxes to *Tricorythodes*, a collector-gatherer mayfly, were lower in guppy reaches than in control reaches. Guppies could have both direct and indirect negative effects on *Tricorythodes* including predation, competition for high quality organic matter between guppies and invertebrates, and alteration of *Tricorythodes* feeding behavior because guppies are present in high densities on patches of fine organic matter. Fluxes of N to beetle and moth grazers (*Psephenus* and *Petrophila*) were usually higher in guppy introduction reaches than in control reaches, with the exception of *Petrophila* populations in control and guppy introduction reaches of the natural canopy stream. Increased primary production in guppy reaches would have increased food availability for grazers, and both species have body types that are unlikely to be susceptible to predation by guppies: *Petrophila* live in cases that are flat and attached to rocks and *Psephenus* (water pennies) have a flat body shape and are tightly attached to rocks.

Removal or addition of vertebrates has had obvious impacts on standing stocks of organic matter in other tropical streams, e.g., grazing tadpoles (Whiles et al. 2013), grazing armored catfish (Capps et al. 2015), or detritivorous fish (Flecker and Taylor 2004, Taylor et al. 2006), but we noted no effects of guppy presence on biofilm biomass or chlorophyll *a* standing stock despite increased primary production in guppy reaches. Since guppies are omnivorous (Zandona et al. 2011), they are also unlikely to exert top-down effects of the same magnitude as a predator. However, our results suggest that effects of guppies on the food web nevertheless exist and that effect sizes are similar to effects of canopy removal. The relative strengths of effects of nutrients, light, and consumers on other aquatic ecosystems are not consistent, with stronger effects of consumers in some systems (e.g., Flecker et al. 2002), but stronger effects of

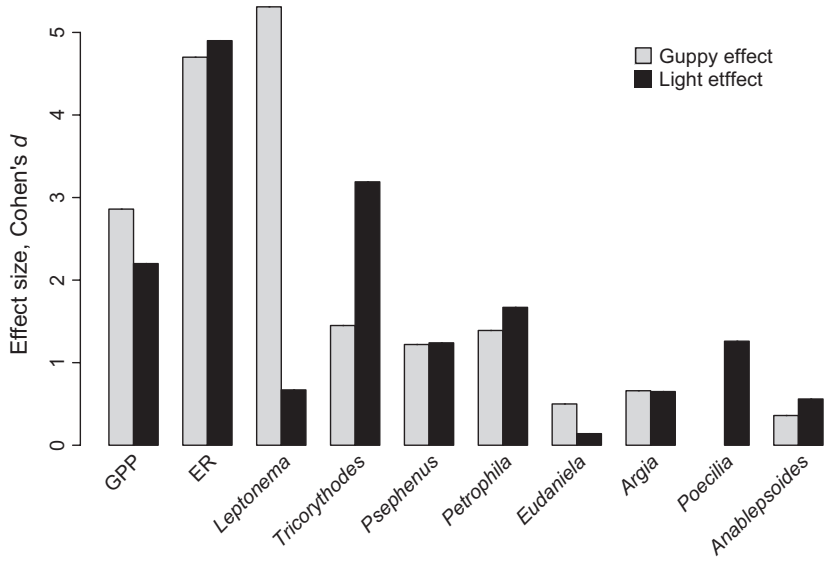

FIG. 4. Effect sizes (Cohen's *d*) from guppy and light treatments on gross primary productivity (GPP), ecosystem respiration (ER), and N flux to consumer taxa.

light or nutrients in others (e.g., Lourenço-Amorim et al. 2014). The relative importance of top-down and bottom-up drivers is likely to depend on the response variable. For example, Rosemond et al. (2001) documented stronger effects of consumers on organic matter cycling, but stronger effects of nutrients on insect biomass. No previous study in streams has used N flux as a response variable, and our results suggest that consumers and light cause responses of similar magnitude, which is consistent with results from previous artificial stream studies in Trinidad (El-Sabaawi et al. 2015).

The large increase in combined N fluxes in the guppy introduction reach of the thinned canopy stream, relative to all other treatments, indicates that the impact of guppies and light are additive. This interaction was not evaluated statistically because it is a sum of all N flux and treatment reaches are not replicated. Interactions between treatments were likely a result of positive effects of canopy thinning and primary production on resources for guppies, which could lead to increased positive effects of guppies on primary production. For example, guppy feeding on detritus could clear the substrate for additional algal growth. Relatively high guppy population estimates in the thinned canopy stream (approximately double the natural canopy stream) also support this idea, and higher guppy density in the thinned canopy stream generally suggests that there are strong interactive effects of light and guppies. Strong interactive effects of consumers and nutrients have also been observed in other streams (e.g., Rosemond et al. 2001, Flecker et al. 2002, Lourenço-Amorim et al. 2014) and lake (e.g., Hillebrand and Kahlert 2001) ecosystems, but effects of consumers and nutrients are often antagonistic rather than synergistic. In Neotropical streams in both Brazil and Venezuela, algal biomass and chlorophyll *a* increase strongly in response to the addition of nutrients, but decline in response to top-down effects of consumers (Flecker et al. 2002, Lourenço-Amorim et al. 2014). Our manipulation of light, rather than nutrients, contrasts with these other previous studies, which focused on increased nutrient availability as a bottom-up driver, perhaps because the two fold increase in light in this study is not as great as the increase in many nutrient addition studies. Food web level effects of light relative to nutrients may not be the same due to interactions between light and nutrients and how they influence food quality (Hill et al. 2010). Generally, the effect of consumers on aquatic ecosystem function can be complex and nonlinear (Klemmer et al. 2012), and the results from this experiment and other studies suggest that the direction and magnitude of the combined effects of consumers, nutrients, and light are highly system specific.

Effects on autotrophic vs. detritus-based linkages

N fluxes to shredder caddisflies (*Phylloicus*), detritivorous crabs (*Eudaniela*), and killifish (*Anablepsoides*) did not differ among light or guppy treatment reaches. Despite the lack of effects, N fluxes to these highly detritivorous taxa span a large range: fluxes of N to *Phylloicus* were low relative to most other primary consumers, fluxes of N to *Eudaniela* were higher than any other taxon. High biomass of crabs relative to other invertebrates was an important component of the magnitude of N flux rates even though crabs have relatively slow turnover rates compared with insects, but crab biomass was highly variable. The high biomass and N flux rates to crabs are consistent with strong effects of macroconsumers relative to shredder insects in other Neotropical streams (Moulton et al. 2010). Similarly, killifish diets are composed of high proportions of detritus (including ~35% dead terrestrial invertebrates; B. Lamphere, *unpublished data*), also suggesting that detrital food web linkages are not as influenced by light or guppy manipulations.

Generally, flux rates indicate that detritivory by macroconsumers is an important pathway in our study system. While we saw strong effects of light and guppies on some invertebrate groups that eat fine organic matter (collector gatherer mayflies and filter feeding caddisflies), fluxes to shredder insects and crabs did not appear to be sensitive to our experimental manipulations. The lack of a fish effect is somewhat surprising since guppy presence in prior mesocosm experiments had a dramatic effect on leaf decomposition (Bassar et al. 2010), but the mechanisms driving this process are poorly understood. The absence of a significant effect on many detritus-based linkages suggests that effects on detritus-based pathways may vary across systems; for example, Rosemond et al. (2001) found that effects of consumers and nutrients on detritivore biomass and detrital processing were stronger than many previously documented effects on grazing pathways. There is evidence, however, that consumers in tropical streams may differentially rely on high-quality algal resources even though they are relatively scarce compared to detrital resources (March and Pringle 2003, Lau et al. 2009), which could have led to stronger effects of light and consumers on groups of consumers that eat a mix of autotrophic and detrital resources. The importance of scarce, but high-quality, algae also agrees with conceptual models developed in temperate systems (e.g., Revised Riverine Productivity Model; Thorp and Delong 2002). Previous survey results from Trinidad streams also support this idea; survey studies found that increased light was associated to increased use of autotrophic resources both within and across consumer species, but did not have a strong effect on shredders (Collins et al. 2016).

Advantages and limitations of a whole-ecosystem experiment

Conducting an experiment at the stream-reach scale presented a unique opportunity to evaluate the effects of fish and light on stream food webs. Replication, however, was necessarily limited because of the intensity of

conducting the ecosystem manipulation and the isotope tracer study. Our statistical contrasts provided strong evidence for differences between reaches, but transects within each reach are pseudoreplicates for the guppy and light manipulations. While we hypothesize that the differences among treatment reaches are a result of guppy introduction and canopy manipulation, we cannot be statistically certain, due to the lack of replication of the whole ecosystem experiment. Replicated mesocosm experiments in Trinidad have also shown strong effects of light and guppies on stream ecosystems (Bassar et al. 2010, El-Sabaawi et al. 2015), further supporting the idea that differences between reaches in our experiment are a result of guppies and light.

This work was conducted in small, wadeable streams (<20 L/s discharge, <3 m wetted width) during the dry season to accommodate the isotope tracer approach. Because of seasonal constraints, we were not able to evaluate the potentially important effects of hydrology. Hydrologic disturbance and seasonal differences in rainfall are critical drivers of food web pathways in our study system in Trinidad (Travis et al. 2014) and in other Neotropical stream ecosystems (Pringle and Hamazaki 1997, Winemiller et al. 2006, Frauendorf et al. 2013), yet hydrology is difficult to control in experiments. Our results may show more pronounced effects of light and guppies than during other time periods; the extent and severity of dry weather in the 2010 dry season was greater than any other year from 2008 to 2011, which led to stable flows and high guppy densities in both streams. In addition to the results presented here, data from mesocosms with controlled flow conditions (e.g., El-Sabaawi et al. 2015) show clear effects of light and guppies, but we suspect that they might be more difficult to detect when hydrologic conditions are more variable.

Conclusions

In summary, these results suggest that bottom-up effects of light and top-down effects of fish introductions have comparable influences on food web fluxes. We identified strong differences between light and guppy treatment on fluxes to many consumer taxa, but they were restricted to functional feeding groups that consume epilithon and benthic or suspended fine organic matter. While this study showed that coarse organic matter makes a major contribution to the energetic budget of these streams, our results showed no effects of our treatments on shredder species. This result suggests that the effects of light and fish introductions on N flux rates may be direct and limited to autotrophic pathways, while possible indirect effects on fluxes to detritivores and predators were minimal or undetectable. The combination of a whole-ecosystem experiment with a stable isotope tracer addition allowed us to extend knowledge about top-down and bottom-up effects to evaluate effects on ecosystem fluxes in natural streams.

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Supporting Information

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